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PHALLI OF RECENT GENERA AND SPECIES OF THE FAMILY GEOMYIDAE (MAMMALIA: RODENTIA)

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ABSTRACT

A study of the external morphology of the phalli and bacula of the family Geomyidae was conducted. All six genera and 24 species (including the nine species of *Thomomys*, the single species of *Zygogeomys*, one of 11 species of *Orthogeomys*, the six species of *Geomys*, one of two species of *Pappogeomys*, and six of seven species of *Cratogeomys*) were examined. Detailed descriptions, with illustrations and measurements, were provided for each taxa. Measurements were used in univariate and multivariate statistics to examine individual, geographical, and interspecific variation. Results of the study were compared to systematic relationships proposed by previous investigators.

INTRODUCTION

Morphological studies of mammalian phalli have been useful in differentiating related taxa (Genoways, 1973; Hoffmeister and Lee, 1963; Hooper, 1958, 1959, 1960, 1961, 1962; Hooper and Hart, 1962; Hooper and Musser, 1964; Lidicker, 1968; Williams et al., 1980). In spite of the numerous investigations that have been conducted on phalli of various mammal groups, such studies dealing with the New World family Geomyidae have been limited.

The phalli of the genus *Thomomys* are the best documented in the family Geomyidae. However, except for studies by Hill (1937) who described the phallus of *T. bulbivorous*, all investigations of *Thomomys* have been concerned with only the baculum and have excluded the soft anatomy of the phallus. Bacula of species of *Thomomys* have received considerably more attention because of their usefulness in differentiating taxa, particularly in restricted geographical areas. Thaeler (1968) discussed bacular differences between *T. bottae*, *T. mazama*, *T. monticola*, and *T. talpoides* in northern California. Bacular differences were also examined between *T. mazama* and *T. talpoides* in western Washington by Johnson and Benson (1960). Long (1964) and Thaeler (1972) discuss differences between the bacula of *T. idahoensis* and *T. talpoides* in eastern Idaho. Bacular differences between *T. bottae* and *T. umbrinus* in southern Arizona have been reported by Hoffmeister (1969) and Patton (1973). The only effort to make a more comprehensive examination of *Thomomys* bacula was made by Burt (1960) in which bacula of *T. bottae*, *T. bulbivorous*, *T. talpoides*, and *T. umbrinus* were described.

In the remaining genera of the family Geomyidae (*Orthogeomys*, *Zygogeomys*, *Geomys*, *Pappogeomys*, and *Cratogeomys*) nothing is known about the external morphology of the phallus except for the brief description of *G. bursarius* by Hill (1937). Furthermore, documentation concerning the bacula of these taxa is very limited. Four of the six species of *Geomys* (*G. attwateri*, *G. bursarius*, *G. personatus*, and *G. pinetis*) have received brief descriptions by Burt (1960), Kennerly (1958), and Sherman (1940). Burt (1960) also briefly described the bacula of *Zygogeomys trichopus* and two of the seven species of *Cratogeomys* (*C. merriami* and *C. tylorhinus*).

Therefore, the current knowledge of phalli in the family Geomyidae is almost entirely restricted to a few descriptions and dimensions of bacula of selected taxa. Information about the soft anatomy of the phallus of all geomyid species (except *T. bulbivorous* and *G. bursarius*) and the bacula of almost half of the species is nonexistent. Furthermore, there is essentially no phallic or bacular information available concerning nongeographical and geographical morphometric variation within a species, or among species of a common genus.

The purpose of this study is to examine and describe the external morphology of the phalli and the bacula of members of the family Geomyidae. It is intended to provide detailed descriptions, measurements, and illustrations for each available taxon. With these data, statistical analyses are performed to assess nongeographical and geographical variation within selected species, followed by examination of variation among species. Information obtained in this study is finally used to discuss possible systematic relationships among the species examined.

METHODS AND MATERIALS

Penes were removed from 388 specimens of geomyid rodents representing all six genera plus 24 species and 80 nominal races. Most penes were removed from freshly killed specimens. Others were removed from study skins maintained in mammal research collections, and subsequently rehydrated. Penes were preserved in a solution of ethyl alcohol, formalin, and acetic acid (AFA).

Because the validity of using dried penes has been previously questioned (Lidicker, 1968), tests were performed to determine the amount of restoration that might be expected from dried penes. Eight penes were removed from fresh pocket gophers and immediately illustrated, using a Wild camera-lucida dissecting scope. Seven of the penes were allowed to dry completely. The eighth sample was placed in AFA. These samples were maintained in this condition for over five years. The dried penes were rehydrated and then all eight samples were illustrated again. The outlines of both illustrations of each sample were placed over each other to observe any alteration in shape and size caused by their respective treatments. The seven dried samples did show some alteration in shape after restoration. However, six of the samples were not any different than similar alterations observed in the sample that was kept in AFA. One dried sample was not restored to its original shape. However, in this case the effects caused by drying were easily detected without comparing illustrations. Therefore it was assumed that any serious distortions caused by drying could be detected by careful examination of the rehydrated sample. Distorted samples are generally compressed laterally; the overall length in adult specimens is not affected because of the support provided by the baculum. For individual samples having distorted phalli, measurements of width of the glans were omitted.

Although all samples were examined, for purposes of final comparisons and analyses only adult individuals were used, thus eliminating variation attributed to age. (To adequately examine age variation considerably larger sample sizes should be available.) Determination of adult specimens was based on the fusion of the basioccipital and basisphenoid bones. For some taxa, such as *Thomomys*, development of sagittal and lambdoidal crests and overall size were also used to determine mature, adult individuals.

Samples were first examined externally to determine characteristic features. In addition to checking each sample from dorsal, ventral, and lateral views, special attention was given to apical and epidermal structures. Within each species individual samples were reexamined, compared, and a description was written for the species. Anatomical terminology used in all descriptions generally follows that of Hooper (1958). Next a representative sample of each species was selected and schematically illustrated, using a Wild camera-lucida dissecting scope. For illustrative purposes each sample was magnified about 12 times for lateral, ventral, and dorsal views, and about 50 times for close-up views of epidermal structures. A metric scale was always included with the lateral, ventral, and dorsal views so that the amount of magnification could be accurately determined.

Individual penes were subsequently cleared and stained (Russell, 1973) so that the size, shape, and position of the baculum could be determined. Because of potential loss of epidermal structures (particularly on dried phalli) caused by clearing and staining, such procedures were performed usually after thorough examination of untreated samples was completed. The bacula were examined and compared, and a description was written for each species. The baculum corresponding to the illustrated glans was also illustrated using the camera-lucida. In each case the magnification was adjusted to the magnification used in the illustration for the glans.

After clearing and staining was completed, measurements were taken of the glans and baculum of each adult specimen. This procedure was followed so that any differences that might exist between fresh and dried penes would be minimized by their common treatment. Because measurements were taken from cleared and stained samples, all samples were examined while they were submerged in glycerin, so that the shape would be natural and problems of dessication would be eliminated. Measurements were taken from magnified outlines of the samples, using the camera-lucida, and dial calipers. Again a metric scale was included in each diagram to determine the exact magnification. Dimensions of the outline were then divided by the magnification to provide the actual dimensions of the sample. Each dimension was rounded to the nearest one-tenth millimeter. Using the described procedure the following measurements were taken:

1. *Length of distal tract*.—Distance of the entire phallus between distalmost point of the glans and the ventral flexure, as measured from the ventral aspect.
2. *Length of glans*.—Distance between the distalmost point of the glans and a midventral point at the connection of the glans and prepuce, as measured from the ventral aspect.
3. *Length of protractile tip*.—Distance between the distalmost point of the glans and a midventral point on the distal edge of the collar, as measured from the ventral aspect.
4. *Width of glans across collar*.—Greatest distance of the glans across collar region, as measured from the ventral aspect.
5. *Width of glans across base*.—Distance of the glans at the constriction where the glans and prepuce conneet, as measured from the ventral aspect.
6. *Length of baculum*.—Distance between the distalmost and proximalmost points of the baculum.
7. *Width of bacular base*.—Greatest distance of the base of the baculum as measured from the ventral aspect.
8. *Height of bacular base*.—Greatest distance of the base of the baculum, as measured from the lateral aspect.

Tests were made to determine if accurate bacular measurements could be made without removing the baculum from the glans, thus potentially destroying the glans. The samples were measured within the glans, removed from the glans, and measured again. Percent differences in measurements of the length, width, and height of 10 dissected bacula were (mean followed by range in parentheses) 3.0 (0.1–10.9), 12.2 (0.0–40.8) and 9.1 (0.6–34.0), respectively. Based on these findings it was assumed that accurate measurements could not be acquired from bacula remaining in the glans. Therefore, all bacular measurements were taken from dissected bacula.

Relative size relationships of phalli and bacula with body size are often examined by utilizing the length of hind foot as a standard (Hooper, 1958, 1959, 1960; Hooper and Hart, 1962; Hooper and Musser, 1964). Because hind foot measurements often lack consistency and precision in documentation, this study substituted condylobasal length as a comparative measurement. However, hind foot lengths were also documented for the benefit of other investigators.

Standard statistics (mean, standard error, and coefficient of variation) of individual nominal taxa were computed with a Texas Instruments SR51-A calculator. Analysis of age variation was not included in this study. However, analyses of individual and geographical variation were included, using adult individuals. For series of samples with three or more individuals a Sum of Squares Simultaneous Test Procedure (SS-STP), developed by Gabriel (1964) and available in a univariate statistical program called UNIVAR (Power, 1970), was used to determine maximally nonsignificant subsets. Because sample sizes and geographical representation were limited in most taxa, the SS-STP analysis was only applied to univariate analysis of geographical variation in the genus *Geomys*.

Multivariate analyses were performed on a DEC-10 computer at Carnegie Mellon University, Pittsburgh. Means of one cranial (condylobasal length), five phallic, and three bacular characters of each species were used in a MINT multivariate analysis to determine phenetic relationships. These relationships were determined by cluster and principal component analyses. Matrices of Q-Mode correlation (among OTU's) and phenetic distance coefficients were computed. Cluster analyses were conducted using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices. A phenogram was generated for each matrix. Phenograms were compared with their respective matrices, and a coefficient of cophenetic correlation was computed. A matrix of Pearson's product-moment correlation coefficient among characters was computed, and the first three principal components extracted. Projections of the OTU's on the first three principal components were made.

Institutions from which material was used on this project, followed by the respective acronym in parentheses, are as follows: Carnegie Museum of Natural History (CM); Florida State Museum, University of Florida (FSM); Museum of Natural History, University of Kansas (KU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); New Mexico State University (NMSU); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); The Museum, Texas Tech University (TTU).

RESULTS

All six genera and 24 species of the family Geomyidae were examined. This study includes the nine species of *Thomomys*—*bottae, bulbivorous, clusius, idahoensis, mazama, monticola, talpoides, townsendii,* and *umbrinus* (see Hall, 1981, plus Anderson, 1966, Hoffmeister, 1969, and Patton, 1973, for use of *T. bottae* and *T. umbrinus*; Thaeler, 1979, for use of *T. clusius*; Thaeler, 1972, for use of *T. idahoensis*; and Hall and Kelson, 1959, and Thaeler, 1980, for use of *T. townsendii*); the single species of *Zygogeomys*—*trichopus* (see Hall, 1981); one of the eleven species of *Orthogeomys*—*hispidus* (see Hall, 1981); the six species of *Geomys*—*arenarius, attwateri, bursarius, personatus, pinetis,* and *tropicalis* (see Hall, 1981, and Williams and Genoways, 1980, for use of *G. pinetis* and synonymizing of *G. colonus, G. cumberlandius,* and *G. fontanelus*; Williams and Genoways, 1981, for taxonomic changes in *G. personatus*; and Tucker and Schmidley, 1981, for use of *G. attwateri*); one of the two species of *Pappogeomys*—*bulleri* (see Hall, 1981, and Honeycutt and Williams, 1982, for use of *Pappogeomys*); and six of the seven species of *Cratogeomys* (see Hall, 1981, and Honeycutt and Williams, 1982, for use of *Cratogeomys*).

The typical geomyid phallus is relatively simple in form. The distal tract is about four to 20 times longer than its width. Somewhere near the middle of the distal tract exists a *constriction* where the prepuce and proximal margin or base of the glans connect. Proximal to the constriction, the distal tract usually expands basally and is essentially featureless. The glans itself possesses several characteristic features. The most conspicuous feature is the *collar* which partially or completely encircles the glans in the vicinity of the urethral opening. This collar may be simple or very elaborate in shape. The collar marks the proximal boundary of the *protractile tip* of the glans. On the ventral side of the protractile tip is a single pair of *urethral processes* which vary in shape and size and connect inside the collar on the ventral wall of the urethral opening. The region between the collar and constriction often possesses more subtle features such as a *midventral raphe* and *middorsal groove*. Occasionally lateral grooves are present and form one or two *dorsal protuberances,* depending on the extent and development of the middorsal groove. Between the collar and constriction characteristic *epidermal structures* are usually present. These structures may also occur on the dorsal side of the protractile tip. Each structure usually has one or more proximally oriented projections which generally occur among minute longitudinal folds and ridges. Epidermal features can easily be seen with magnification. Individual structures may be arranged in an uniform or irregular pattern with respect to other structures. The regions proximal to the constriction and on the ventral and lateral sides of the protractile tip are usually void of such epidermal structures.

The baculum of geomyid rodents is positioned between the central axis and dorsal side of the phallus. It extends into the protractile tip of the glans and runs posteriorly into the area proximal to the constriction. The baculum is entirely osseous and usually consists of an enlarged base that tapers into a long shaft that terminates with a distinct tip. The baculum is typically curved with the dorsal side being concave.

The following are more detailed descriptions about the phalli and bacula of specific taxonomic groups, at the generic level followed by descriptions of represented species.

Thomomys

Description

Species belonging to the genus *Thomomys* show remarkable variation in the size and shape of the phallus. The length of the distal tract of adult specimens examined ranged from 10.7 to 34.1 mm. The length of the distal tract compared to relative body size of individuals is very different among species, with ratios of the condylobasal length to the length of the distal tract ranging from 1.1 to 4.2. Basically the shape of the phallus of individual species falls into one of two types—either long and narrow, or short to medium and broad. Depending on the species, typical features, such as the constriction, collar, and urethral processes, may vary from visible complexity to being simple and less distinct. Other features such as raphe, middorsal grooves, dorsal protuberances, and epidermal structures may or may not exist—again depending on the species considered.

The baculum is equally variable in size and is directly related to the length of the distal tract. Basically the shape and structure are typical for geomyid rodents. The ratios of the condylobasal length and length of the distal tract to the length of the baculum ranges from 1.1 to 5.7 and 1.0 to 1.5, respectively. Bacular lengths ranged from 9.1 to 32.9 mm in adult specimens examined.

The following are detailed descriptions of the nine recognized species of *Thomomys—T. bottae, T. bulbivorous, T. clusius, T. idahoensis, T. mazama, T. monticola, T. talpoides, T. townsendii,* and *T. umbrinus*. Table 1 provides the measurements that apply to each description.

Thomomys bottae.—The shape and size of the phallus of *T. bottae* (Fig. 1) agrees with the general description of the phallus of geomyid rodents. However, compared to other species of *Thomomys* the size of the phallus would be considered small to medium-sized, with the length of the distal tract of adult specimens examined ranging from 12.4 to 16.7 mm. The length of the distal tract is four to five times greater than its width. The length of the glans is less than half the length of the distal tract. The sides of the glans are more or less parallel between the collar and constriction, and are generally straight or slightly recurved. The collar region tends to be slightly expanded and is distinct from all aspects. The pair of urethral processes are exposed and well-developed. Other features present on the glans include a raphe that may vary in distinctness among individuals, and a well-developed middorsal groove that may extend almost the full length of the glans. Between the collar and constriction there is a pair of conspicuous dorsal protuberances.

Epidermal structures have a single proximally oriented projection. The structures are generally fairly uniform in shape, size, and pattern.

The shape of the baculum (Fig. 1) is typical of most geomyid rodents, with a distinct base and tip and distally tapering, and slightly curved shaft. The length of the baculum among adults examined ranged from 10.2 to 14.6 mm. The width of the base tends to be less or equal to the height, and is slightly tapered proximally when viewed dorsoventrally. The description and measurements of the baculum of *T. bottae* examined in this study correspond closely to those found by other investigators (Burt, 1960; Hoffmeister, 1969; Ingles, 1965; Long and Frank, 1968; Patton, 1973; Thaeler, 1968). However, this study examined only eastern subspecies of *T. bottae* in which bacular measurements tended to be larger than those reported of western races of *T. bottae* (Burt, 1960; Ingles, 1965).

The ratios of condylobasal length to the length of distal tract and to length of baculum ranged from 2.2 to 3.3 and 3.0 to 4.0, respectively. The ratio of the length of distal tract to the length of baculum ranged from 3.0 to 4.0.

Specimens examined.—Total (26).

T. b. actuosus (1).—NEW MEXICO: *Torrance Co.:* Red Canyon, 1 (TTU).

T. b. connectens (4).—NEW MEXICO: *Bernalillo Co.:* Jct. Hwy. 500 and Hwy. 85, 1 (TTU); *Torrance Co.:* Willard, 2 (TTU); *Valencia Co.:* Los Lunas, 1 (TTU).

T. b. limitaris (12).—TEXAS: *Brewster Co.:* 18.6 mi N, 1.2 mi E Marathon, 4,300 ft, 6 (TTU); 17.9 mi N, 0.3 mi E Marathon, 4,300 ft, 1 (TTU); *Crockett Co.:* 15 mi N, 11 mi W Ozona, 1 (TTU); 17 mi (by road) NW Ozona, 1 (TTU); *Pecos Co.:* 17.0 mi N, 18.5 mi E Marathon, 4,500 ft, 1 (CM); *Reagan Co.:* 6 mi (by road) SE Stiles, 1 (TTU); *Sutton Co.:* Sonora cemetery, 1 (TTU).

T. b. limpiae (2).—TEXAS: *Jeff Davis Co.:* 10 mi NE Fort Davis, 2 (TTU).

T. b. opulentus (5).—NEW MEXICO: *Socorro Co.:* 1 mi E San Antonio, 5 (TTU).

Table 1.—*Standard statistics for adult specimens of 31 samples representing the nine species of* Thomomys.

Taxon	N	Mean	(Range) ± 2 SE	CV
		Length of distal tract		
Thomomys bottae actuosus	1	14.5		
Thomomys bottae connectens	4	15.7	(15.0–16.7) ± 0.73	4.6
Thomomys bottae limitaris	8	13.4	(12.4–15.8) ± 0.73	7.5
Thomomys bottae limpiae	2	15.1	(14.6–15.7) ± 1.10	5.1
Thomomys bottae opulentus	5	12.6	(12.5–12.8) ± 0.11	1.0
Thomomys bottae ruidosae	2	14.1	(13.9–14.3) ± 0.40	2.0
Thomomys bulbivorous	7	13.5	(11.3–14.5) ± 0.82	8.1
Thomomys clusius	5	12.3	(11.9–12.7) ± 0.31	2.8
Thomomys idahoensis confinus				
Thomomys idahoensis idahoensis				
Thomomys idahoensis pygmaeus				
Thomomys mazama mazama	6	29.8	(27.2–34.1) ± 2.11	8.7
Thomomys monticola	9	15.6	(15.0–16.4) ± 0.39	3.7
Thomomys talpoides bridgeri	5	17.2	(16.4–18.0) ± 0.60	3.9
Thomomys talpoides devexus	1	16.7		
Thomomys talpoides fossor	3	24.4	(23.3–26.2) ± 1.82	6.4
Thomomys talpoides fuscus	1	14.6		
Thomomys talpoides quadratus	2	14.1	(14.0–14.3) ± 0.30	1.5
Thomomys talpoides rostralis	1	21.9		
Thomomys talpoides rufescens	1	20.0		
Thomomys talpoides saturatus	1	20.2		
Thomomys talpoides talpoides	1	19.1		
Thomomys talpoides tenellus	1	21.8		
Thomomys townsendii bachmani	3	13.5	(13.0–14.0) ± 0.58	3.7
Thomomys townsendii similis	3	14.9	(14.8–15.0) ± 0.13	0.8
Thomomys townsendii townsendii	1	15.5		
Thomomys umbrinus intermedius	2	10.9	(10.7–11.2) ± 0.41	9.2
Thomomys umbrinus juntae	1	10.3		
Thomomys umbrinus madrensis	1	10.5		
Thomomys umbrinus sheldoni	3	11.1	(11.0–11.3) ± 0.20	1.6
Thomomys umbrinus spp.	2	12.1	(11.9–12.3) ± 0.40	2.3
		Length of glans		
Thomomys bottae actuosus	1	7.5		
Thomomys bottae connectens	4	7.9	(7.4–8.3) ± 0.42	5.3
Thomomys bottae limitaris	8	6.9	(5.9–8.7) ± 0.59	12.1
Thomomys bottae limpiae	2	8.1	(7.8–8.3) ± 0.50	4.4
Thomomys bottae opulentus	5	6.8	(6.3–7.7) ± 0.51	8.4
Thomomys bottae ruidosae	2	6.6	(6.4–6.8) ± 0.40	4.3
Thomomys bulbivorous	7	7.7	(6.6–8.5) ± 0.51	8.8
Thomomys clusius	5	7.5	(6.6–8.3) ± 0.56	8.4
Thomomys idahoensis confinus				
Thomomys idahoensis idahoensis				
Thomomys idahoensis pygmaeus				
Thomomys mazama mazama	6	17.7	(16.0–19.3) ± 1.09	7.6
Thomomys monticola	7	8.3	(7.6–9.4) ± 0.49	7.8
Thomomys talpoides bridgeri	5	8.3	(7.4–9.3) ± 0.73	9.8
Thomomys talpoides devexus	1	9.7		
Thomomys talpoides fossor	3	11.7	(10.6–13.0) ± 1.39	10.3
Thomomys talpoides fuscus	1	8.7		
Thomomys talpoides quadratus	2	7.1	(6.6–7.7) ± 1.10	10.9
Thomomys talpoides rostralis	1	12.4		
Thomomys talpoides rufescens	1	9.6		
Thomomys talpoides saturatus	1	9.4		
Thomomys talpoides talpoides	1	9.9		
Thomomys talpoides tenellus	1	11.0		
Thomomys townsendii bachmani	3	7.3	(6.6–7.7) ± 0.68	8.0
Thomomys townsendii similis	3	7.5	(7.5–7.5) ± 0.00	0.0

Table 1.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Thomomys townsendii townsendii	2	7.8	(7.7–7.8) ± 0.20	1.8
Thomomys umbrinus intermedius	3	5.7	(4.7–6.3) ± 0.98	14.9
Thomomys umbrinus juntae	1	5.1		
Thomomys umbrinus madrensis	1	5.7		
Thomomys umbrinus sheldoni	3	6.2	(5.7–6.5) ± 0.48	6.7
Thomomys umbrinus spp.	2	6.5	(6.5–6.6) ± 0.10	1.1
		Length of protractile tip		
Thomomys bottae actuosus	1	3.3		
Thomomys bottae connectens	4	3.5	(2.7–4.1) ± 0.60	17.1
Thomomys bottae limitaris	8	3.1	(2.9–3.5) ± 0.17	7.7
Thomomys bottae limpiae	2	3.7	(3.6–3.9) ± 0.30	5.7
Thomomys bottae opulentus	5	3.1	(2.6–3.7) ± 0.37	13.4
Thomomys bottae ruidosae	2	2.5	(2.5–2.6) ± 0.10	2.8
Thomomys bulbivorous	7	3.3	(2.3–4.2) ± 0.55	22.0
Thomomys clusius	5	3.8	(3.4–4.3) ± 0.34	10.1
Thomomys idahoensis confinus				
Thomomys idahoensis idahoensis				
Thomomys idahoensis pygmaeus				
Thomomys mazama mazama	6	2.7	(1.8–3.3) ± 0.56	25.4
Thomomys monticola	7	3.5	(2.8–4.0) ± 0.35	13.2
Thomomys talpoides bridgeri	5	4.8	(4.3–5.9) ± 0.60	14.1
Thomomys talpoides devexus	1	3.7		
Thomomys talpoides fossor	3	4.4	(3.7–5.4) ± 1.05	20.6
Thomomys talpoides fuscus	1	3.1		
Thomomys talpoides quadratus	2	3.7	(3.2–4.1) ± 0.90	17.2
Thomomys talpoides rostralis	1	5.3		
Thomomys talpoides rufescens	1	4.9		
Thomomys talpoides saturatus	1	3.9		
Thomomys talpoides talpoides	1	4.5		
Thomomys talpoides tenellus	1	3.7		
Thomomys townsendii bachmani	3	3.2	(2.9–3.1) ± 0.48	13.0
Thomomys townsendii similis	3	3.4	(3.2–3.6) ± 0.24	6.1
Thomomys townsendii townsendii	2	3.2	(2.7–3.7) ± 1.00	22.1
Thomomys umbrinus intermedius	3	2.5	(2.0–2.9) ± 0.55	18.9
Thomomys umbrinus juntae	1	2.6		
Thomomys umbrinus madrensis	1	2.2		
Thomomys umbrinus sheldoni	3	2.7	(2.3–3.1) ± 0.46	14.8
Thomomys umbrinus ssp.	2	3.1	(3.0–3.3) ± 0.30	6.8
		Width of glans across collar		
Thomomys bottae actuosus	1	2.3		
Thomomys bottae connectens	4	2.7	(2.3–3.0) ± 0.30	11.1
Thomomys bottae limitaris	8	2.3	(1.9–2.9) ± 0.26	15.9
Thomomys bottae limpiae	2	3.0	(2.9–3.1) ± 0.20	4.7
Thomomys bottae opulentus	5	2.8	(1.9–3.5) ± 0.61	24.3
Thomomys bottae ruidosae	2	1.9	(1.6–2.2) ± 0.60	22.3
Thomomys bulbivorous	7	3.7	(2.9–4.5) ± 0.41	14.6
Thomomys clusius	5	3.2	(2.6–3.7) ± 0.42	14.6
Thomomys idahoensis confinus				
Thomomys idahoensis idahoensis				
Thomomys idahoensis pygmaeus				
Thomomys mazama mazama	6	2.5	(1.9–3.0) ± 0.43	21.1
Thomomys monticola	5	2.4	(1.7–3.2) ± 0.54	25.3
Thomomys talpoides bridgeri	5	2.2	(1.8–2.5) ± 0.25	13.0
Thomomys talpoides devexus				
Thomomys talpoides fossor	3	2.2	(2.0–2.4) ± 0.24	9.5
Thomomys talpoides fuscus	1	1.9		
Thomomys talpoides quadratus	2	2.6	(2.6–2.6) ± 0.00	0.0

Table 1.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Thomomys talpoides rostralis	1	3.2		
Thomomys talpoides rufescens	1	2.8		
Thomomys talpoides saturatus	1	1.7		
Thomomys talpoides talpoides	1	1.8		
Thomomys talpoides tenellus	1	1.8		
Thomomys townsendii bachmani	3	3.0	(2.9–3.1) ± 0.11	3.3
Thomomys townsendii similis	3	2.7	(2.6–2.8) ± 0.13	4.3
Thomomys townsendii townsendii	2	2.7	(2.2–3.2) ± 1.00	26.2
Thomomys umbrinus intermedius	3	2.2	(1.5–2.5) ± 0.67	26.2
Thomomys umbrinus juntae	1	4.1		
Thomomys umbrinus madrensis	1	2.0		
Thomomys umbrinus sheldoni	2	2.7	(2.2–3.1) ± 0.90	23.6
Thomomys umbrinus ssp.	2	3.3	(2.9–3.8) ± 0.90	19.3
		Width of glans across base		
Thomomys bottae actuosus	1	1.7		
Thomomys bottae connectens	4	2.5	(2.2–2.7) ± 0.21	8.2
Thomomys bottae limitaris	8	1.9	(1.7–2.4) ± 0.16	12.3
Thomomys bottae limpiae	2	2.4	(2.3–2.5) ± 0.20	5.9
Thomomys bottae opulentus	5	2.1	(1.5–2.8) ± 0.47	24.8
Thomomys bottae ruidosae	2	1.7	(1.7–1.7) ± 0.00	0.0
Thomomys bulbivorous	7	3.7	(3.2–4.3) ± 0.38	13.5
Thomomys clusius	5	2.1	(1.9–2.3) ± 0.13	7.1
Thomomys idahoensis confinus				
Thomomys idahoensis idahoensis				
Thomomys idahoensis pygmaeus				
Thomomys mazama mazama	6	3.0	(2.6–3.3) ± 0.20	8.2
Thomomys monticola	5	1.8	(1.5–2.3) ± 0.35	21.7
Thomomys talpoides bridgeri	5	2.2	(2.0–2.4) ± 0.13	6.7
Thomomys talpoides devexus				
Thomomys talpoides fossor	3	1.9	(1.7–2.0) ± 0.18	8.0
Thomomys talpoides fuscus	1	1.7		
Thomomys talpoides quadratus	2	2.1	(2.0–2.1) ± 0.10	3.4
Thomomys talpoides rostralis	1	2.4		
Thomomys talpoides rufescens	1	2.3		
Thomomys talpoides saturatus	1	1.7		
Thomomys talpoides talpoides	1	1.9		
Thomomys talpoides tenellus	1	2.0		
Thomomys townsendii bachmani	3	2.7	(2.5–2.9) ± 0.24	7.7
Thomomys townsendii similis	3	2.1	(2.0–2.3) ± 0.18	7.3
Thomomys townsendii townsendii	2	2.5	(2.1–2.9) ± 0.80	22.6
Thomomys umbrinus intermedius	3	2.1	(1.4–2.5) ± 0.73	30.2
Thomomys umbrinus juntae	1	2.6		
Thomomys umbrinus madrensis	1	2.0		
Thomomys umbrinus sheldoni	2	2.3	(1.8–2.7) ± 0.90	27.7
Thomomys umbrinus ssp.	2	2.5	(2.2–2.9) ± 0.70	19.8
		Length of baculum		
Thomomys bottae actuosus	1	11.3		
Thomomys bottae connectens	4	13.1	(11.1–14.6) ± 1.54	11.8
Thomomys bottae limitaris	8	11.4	(10.3–13.1) ± 0.69	8.6
Thomomys bottae limpiae	2	11.2	(11.0–11.4) ± 0.40	2.5
Thomomys bottae opulentus	5	10.8	(10.2–11.7) ± 0.55	5.7
Thomomys bottae ruidosae	1	11.9		
Thomomys bulbivorous	5	10.1	(9.6–10.3) ± 0.26	2.9
Thomomys clusius	5	11.3	(10.0–12.1) ± 0.71	7.0
Thomomys idahoensis confinus	1	16.2		
Thomomys idahoensis idahoensis	6	21.5	(20.0–23.4) ± 1.04	5.9
Thomomys idahoensis pygmaeus	4	19.6	(17.8–21.0) ± 1.34	6.8

Table 1.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Thomomys mazama mazama	5	28.2	(24.9–32.9) ± 2.46	10.7
Thomomys monticola	5	14.6	(13.8–15.2) ± 0.48	3.7
Thomomys talpoides bridgeri	5	15.8	(14.7–16.5) ± 0.63	4.4
Thomomys talpoides devexus	1	15.7		
Thomomys talpoides fossor	3	21.7	(21.1–22.6) ± 0.92	3.7
Thomomys talpoides fuscus	1	13.1		
Thomomys talpoides quadratus	2	12.8	(12.3–13.3) ± 1.03	5.7
Thomomys talpoides rostralis	1	20.1		
Thomomys talpoides rufescens	1	18.7		
Thomomys talpoides saturatus	1	18.0		
Thomomys talpoides talpoides	1	18.2		
Thomomys talpoides tenellus	1	20.5		
Thomomys townsendii bachmani	3	12.5	(12.2–12.7) ± 0.29	2.0
Thomomys townsendii similis	3	13.6	(13.3–13.9) ± 0.35	2.2
Thomomys townsendii townsendii	2	13.5	(13.5–13.6) ± 0.10	0.5
Thomomys umbrinus intermedius	1	8.0		
Thomomys umbrinus juntae	1	9.1		
Thomomys umbrinus madrensis				
Thomomys umbrinus sheldoni	3	9.6	(9.1–10.6) ± 0.97	8.7
Thomomys umbrinus ssp.	2	10.5	(10.0–11.1) ± 1.10	7.4
		Width of bacular base		
Thomomys bottae actuosus	1	1.4		
Thomomys bottae connectens	4	1.7	(1.6–2.0) ± 0.17	10.2
Thomomys bottae limitaris	8	1.5	(1.0–1.8) ± 0.19	17.6
Thomomys bottae limpiae	2	1.5	(1.4–1.6) ± 0.20	9.4
Thomomys bottae opulentus	5	1.3	(1.0–1.6) ± 0.19	16.7
Thomomys bottae rudiosae	1	1.3		
Thomomys bulbivorous	5	2.2	(1.7–2.5) ± 0.26	13.4
Thomomys clusius	5	1.6	(1.4–1.9) ± 0.19	13.5
Thomomys idahoensis confinus	1	1.1		
Thomomys idahoensis idahoensis	6	1.4	(1.3–1.5) ± 0.61	5.4
Thomomys idahoensis pygmaeus	3	1.2	(1.1–1.3) ± 0.13	9.9
Thomomys mazama mazama	5	1.6	(1.3–2.1) ± 0.23	17.7
Thomomys monticola	5	1.6	(1.2–2.0) ± 0.26	18.2
Thomomys talpoides bridgeri	5	1.8	(1.4–2.0) ± 0.22	13.9
Thomomys talpoides devexus	1	1.9		
Thomomys talpoides fossor	3	1.7	(1.7–1.8) ± 0.07	3.4
Thomomys talpoides fuscus	1	1.1		
Thomomys talpoides quadratus	2	1.4	(1.4–1.4) ± 0.00	0.0
Thomomys talpoides rostralis	1	2.4		
Thomomys talpoides rufescens	1	1.6		
Thomomys talpoides saturatus	1	1.7		
Thomomys talpoides talpoides	1	1.7		
Thomomys talpoides tenellus	1	1.4		
Thomomys townsendii bachmani	3	1.1	(0.9–1.2) ± 0.18	13.9
Thomomys townsendii similis	3	1.5	(1.5–1.5) ± 0.00	0.0
Thomomys townsendii townsendii	2	2.3	(2.2–2.4) ± 0.20	6.1
Thomomys umbrinus intermedius	1	0.9		
Thomomys umbrinus juntae	1	2.0		
Thomomys umbrinus madrensis				
Thomomys umbrinus sheldoni	3	1.7	(1.4–2.0) ± 0.35	18.0
Thomomys umbrinus ssp.	2	1.7	(1.6–1.7) ± 0.10	4.1
		Height of bacular base		
Thomomys bottae actuosus	1	1.4		
Thomomys bottae connectens	4	2.0	(1.6–2.4) ± 0.34	16.8
Thomomys bottae limitaris	8	1.8	(1.4–2.0) ± 0.13	10.6
Thomomys bottae limpiae	2	1.5	(1.2–1.7) ± 0.50	23.6

Table 1.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Thomomys bottae opulentus	5	1.3	(1.2–1.8) ± 0.23	20.1
Thomomys bottae ruidosae	1	1.5		
Thomomys bulbivorous	5	2.1	(1.9–2.3) ± 0.15	7.8
Thomomys clusius	5	1.7	(1.4–1.9) ± 0.19	12.5
Thomomys idahoensis confinus	1	0.9		
Thomomys idahoensis idahoensis	6	1.4	(1.2–1.8) ± 0.17	15.1
Thomomys idahoensis pygmaeus	3	1.1	(0.9–1.2) ± 0.18	14.3
Thomomys mazama mazama	5	1.4	(1.0–1.9) ± 0.24	20.9
Thomomys monticola	5	1.6	(1.4–2.0) ± 0.22	15.6
Thomomys talpoides bridgeri	5	1.5	(1.4–1.7) ± 0.10	7.6
Thomomys talpoides devexus	1	1.7		
Thomomys talpoides fossor	3	1.5	(1.1–1.8) ± 0.44	25.2
Thomomys talpoides fuscus	1	1.6		
Thomomys talpoides quadratus	2	1.5	(1.5–1.6) ± 0.10	4.7
Thomomys talpoides rostralis	1	1.8		
Thomomys talpoides rufescens	1	1.9		
Thomomys talpoides saturatus	1	1.5		
Thomomys talpoides talpoides	1	1.6		
Thomomys talpoides tenellus	1	1.8		
Thomomys townsendii bachmanii	3	2.1	(2.0–2.1) ± 0.07	2.7
Thomomys townsendii similis	3	1.9	(1.9–1.9) ± 0.00	0.0
Thomomys townsendii townsendii	2	1.9	(1.9–2.0) ± 0.10	3.7
Thomomys umbrinus intermedius	1	0.9		
Thomomys umbrinus juntae	1	2.0		
Thomomys umbrinus madrensis				
Thomomys umbrinus sheldoni	3	1.7	(1.6–1.9) ± 0.18	9.0
Thomomys umbrinus ssp.	2	1.7	(1.6–1.8) ± 0.20	8.3
		Condylobasal length		
Thomomys bottae actuosus	1	42.1		
Thomomys bottae connectens	4	43.9	(37.1–48.9) ± 5.71	13.0
Thomomys bottae limitaris	8	37.3	(34.0–40.9) ± 1.74	6.6
Thomomys bottae limpiae	2	38.7	(38.1–39.2) ± 1.10	2.0
Thomomys bottae opulentus	5	40.8	(38.8–42.0) ± 1.19	3.3
Thomomys bottae ruidosae	2	37.7	(37.1–38.3) ± 1.20	2.3
Thomomys bulbivorous	7	54.6	(42.4–57.4) ± 1.29	3.1
Thomomys clusius	5	31.6	(30.4–33.0) ± 0.91	3.2
Thomomys idahoensis confinus	1	34.5		
Thomomys idahoensis idahoensis	6	32.2	(31.0–33.3) ± 0.34	2.6
Thomomys idahoensis pygmaeus	4	30.1	(29.4–30.5) ± 0.23	1.5
Thomomys mazama mazama	6	35.9	(34.7–36.7) ± 0.73	2.5
Thomomys monticola	9	35.1	(33.9–36.4) ± 0.47	2.0
Thomomys talpoides bridgeri	5	34.5	(32.5–35.7) ± 1.07	3.5
Thomomys talpoides devexus	1	36.1		
Thomomys talpoides fossor	3	39.1	(37.2–40.3) ± 1.92	4.3
Thomomys talpoides fuscus	1	35.6		
Thomomys talpoides quadratus	2	34.5	(34.2–34.7) ± 0.50	1.0
Thomomys talpoides rostralis	1	36.7		
Thomomys talpoides rufescens	1	39.6		
Thomomys talpoides saturatus	1	34.9		
Thomomys talpoides talpoides	1	38.5		
Thomomys talpoides tenellus	1	37.3		
Thomomys townsendii bachmani	3	47.6	(47.0–48.2) ± 0.70	1.3
Thomomys townsendii similis	3	51.0	(49.8–52.0) ± 1.28	2.2
Thomomys townsendii townsendii	2	50.3	(48.2–52.5) ± 4.31	6.0
Thomomys umbrinus intermedius	3	36.8	(36.3–37.6) ± 0.81	5.4
Thomomys umbrinus juntae	1	38.7		
Thomomys umbrinus madrensis	1	37.7		
Thomomys umbrinus sheldoni	3	39.0	(38.2–40.2) ± 1.20	2.7
Thomomys umbrinus ssp.	2	40.3	(39.6–40.9) ± 1.30	2.3

Table 1.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
		Length of hind foot		
Thomomys bottae actuosus	1	27		
Thomomys bottae connectens	4	30.7	(29–33) ± 2.06	6.7
Thomomys bottae limitaris	8	26.0	(24–29) ± 1.19	6.5
Thomomys bottae limpiae	2	28.0	(27–29) ± 2.01	5.1
Thomomys bottae opulentus	4	31.0	(30–32) ± 0.82	2.6
Thomomys bottae ruidosae	2	25.0	(24–26) ± 2.01	5.7
Thomomys bulbivorous	7	41.1	(39–45) ± 1.47	4.7
Thomomys clusius	5	20.4	(20–21) ± 0.49	2.7
Thomomys idahoensis confinus	1	25		
Thomomys idahoensis idahoensis	6	23.3	(23–24) ± 0.42	2.2
Thomomys idahoensis pygmaeus	4	21.3	(21–22) ± 0.50	2.3
Thomomys mazama mazama	6	28.0	(27–29) ± 0.52	2.3
Thomomys monticola	9	28.7	(27–30) ± 0.58	3.0
Thomomys talpoides bridgeri	5	28.4	(27–29) ± 0.80	3.1
Thomomys talpoides devexus	1	29		
Thomomys talpoides fossor	3	26.7	(24–31) ± 4.38	14.2
Thomomys talpoides fuscus	1	28		
Thomomys talpoides quadratus	2	26.5	(26–27) ± 1.00	2.7
Thomomys talpoides rostralis	1	27		
Thomomys talpoides rufescens	1	30		
Thomomys talpoides saturatus	1	28		
Thomomys talpoides talpoides	1	31		
Thomomys talpoides tenellus	1	28		
Thomomys townsendii bachmani	2	36.0	(36–36) ± 0.00	0.0
Thomomys townsendii similis	3	38.7	(38–39) ± 0.67	1.5
Thomomys townsendii townsendii	2	38.5	(37–40) ± 3.01	5.5
Thomomys umbrinus intermedius	3	29.7	(29–30) ± 0.67	5.0
Thomomys umbrinus juntae	1	29		
Thomomys umbrinus madrensis	1	29		
Thomomys umbrinus sheldoni	3	28.7	(28–29) ± 0.67	2.0
Thomomys umbrinus ssp.	2	30.5	(29–32) ± 3.01	6.9

T. b. ruidosae (2).—NEW MEXICO: *Otero Co.:* 14 mi S, 1 mi E Cloudcroft, 2 (TTU).

Thomomys bulbivorous.—Although the phallus of *T. bulbivorous* (Fig. 2) would be considered short and broad like *T. bottae*, the shape and characteristic features are distinctly unique from all other geomyid species. The length of the distal tract, averaging 13.5 mm and ranging from 11.3 to 14.5 mm in seven adult specimens examined, is small compared to other species. Measurements of the length of distal tract in this study differ from the 18.0 mm reported by Hill (1937), but the phallus of his specimen was evidently over-extended and then measured. The length of the distal tract is three to four times greater than its width, with the glans being more than half the length of the distal tract. Proximal to the constriction the phallus has a bulbous shape. Distally, the glans has converging concave sides, when viewed from a dorsoventral aspect. When viewed from a lateral aspect the sides are more or less straight and parallel. Except for the midventral region, the collar of the glans is unusually large and well-developed, and distinct from all aspects. The urethral processes are also unique among geomyid rodents. The main portion of the urethral processes is exposed, well-developed, and partially connected along their common side. Unlike other members of the family each process possesses a smaller, yet conspicuous, projection on the ventral surface. The region between the collar and constriction also possesses some unique features. For instance, instead of possessing minute longitudinal grooves as in most other geomyid rodents, *T. bulbivorous* possesses an erratic pattern of crevices. The distribution of these crevices is predominantly lateral and ventral, except midventrally where the absence of such crevices gives an indication of the existence of a midventral raphae. Dorsally the crevices tend to form grooves that converge, but then fade out toward the lower middorsal

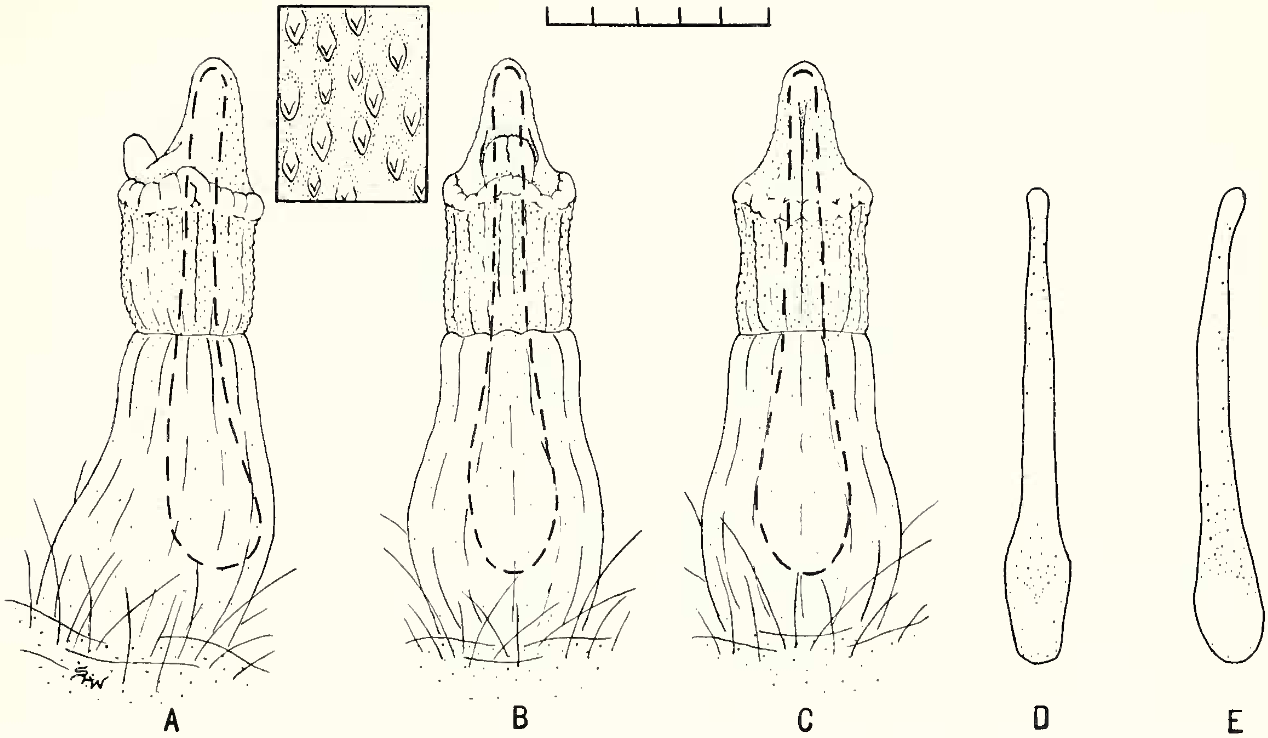

Fig. 1.—Phallus and baculum of *Thomomys bottae opulentus* from New Mexico: Socorro Co., 1 mi E San Antonio (TTU 26433). Illustrated are the lateral (A), ventral (B), and dorsal (C) views of the phallus, magnified view of epidermal structures (enclosed in rectangle) occurring on the glans, and ventral (D) and lateral (E) views of the baculum. The dotted lines in A, B, and C indicate the position of the baculum in the phallus (scale is five millimeters).

region of the glans. In this area the separation of the glans from the proximal portion of the distal tract is not evident. Similarly on the ventral side the midventral region possesses a smaller but more conspicuous "bridge" between the proximal and distal portions of the distal tract. The middorsal groove is restricted to only the collar. Dorsal protuberances do not occur in *T. bulbivorous*.

Epidermal structures have a small, single proximally oriented projection. The size and distribution of these structures are irregular. The structures may be distributed in small clusters.

Although the general shape of the baculum of *T. bulbivorous* (Fig. 2) is typical of geomyid rodents, it does possess a broad tip and a large bulbous base. The width of the base is about the same size as the height. The length of the baculum among seven adult individuals examined averaged 10.1 mm and ranged from 9.6 to 10.3 mm. Burt (1960) and Ingles (1965) reported shorter bacular measurements of 8.5 and 8.8 mm, respectively.

For five specimens the mean and range (in parentheses) of ratios of the condylobasal length to the length of the distal tract and the length of baculum were 4.0 (3.7–4.2) and 5.5 (5.3–5.7), respectively. The ratio of the length of the distal tract to length of baculum averaged 1.4 with a range from 1.3 to 1.5.

Specimens examined.—Total (11).

T. bulbivorous (11).—OREGON: *Benton Co.:* 5 mi N, 5 mi E Corvallis, 200 ft, 2 (CM); 4.5 mi N, 4.5 mi E Corvallis, 1 (TTU); 4 mi NE Corvallis, 7 (CM); Corvallis, 1 (TTU).

Thomomys clusius.—The phallus of *T. clusius* (Fig. 3) is similar to that of *T. bottae,* except that the length of the glans tends to be longer and make up a greater portion of the distal tract. The length of the distal tract, ranging from 11.9 to 12.7 mm in five adults examined, is about four to five times greater than the width, and about two times greater than the length of the glans. The sides of the glans gradually expand distally and flare outward at the well-developed collar. The urethral processes are large and conspicuous. A midventral raphe is pres-

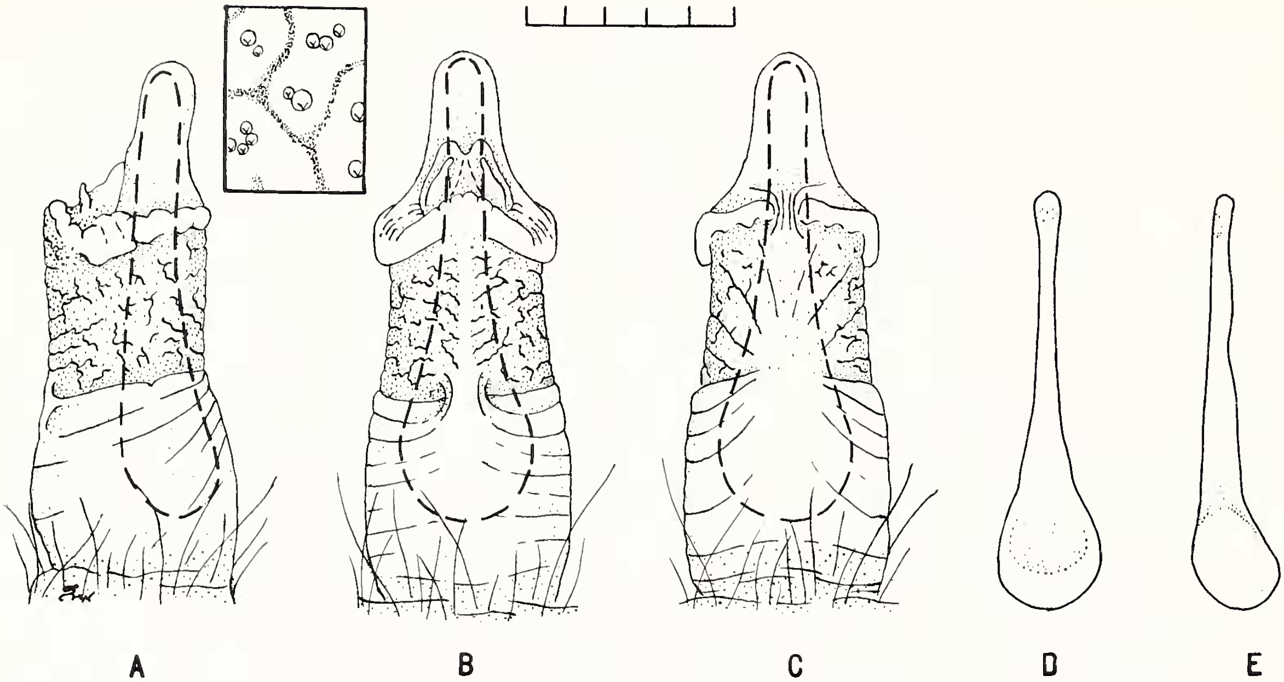

Fig. 2.—Phallus and baculum of *Thomomys bulbivorous* from Oregon: Benton Co., Corvallis (TTU 22816), illustrated as in Fig. 1.

ent as well as a middorsal groove. However, the latter does not extend the entire length of the glans and is most evident in the vicinity of the collar. The dorsal protuberances are not evident.

Epidermal structures, examined on cleared phalli, have single proximally oriented projections. The size, shape, and pattern of the structures are fairly uniform.

The baculum of *T. clusius* (Fig. 3) resembles that of *T. bottae*, although the size of the former tends to be smaller. The length of the baculum of five adults examined ranged from 10.0 to 12.1 mm. The width of the base is about equal to, or slightly smaller than the height of the base. The base is distinct and is slightly tapered proximally.

Comparing five individuals, the average ratios, followed by ranges (in parentheses), of the condylobasal length to length of distal tract and length of baculum, and length of distal tract to length of baculum are 2.6 (2.5–2.7), 2.8 (2.6–3.1), and 1.1 (1.0–1.2), respectively.

Specimens examined.—Total (5).

T. clusius (5).—WYOMING: *Carbon Co.:* 14.4 mi S, 6.0 mi E Rawlins, 6,900 ft, T19N R86W Sec 31, 2 (NMSU); *Sweetwater Co.:* 1.0 mi S, 0.6 mi W Bitter Creek, 6,850 ft, T18N R99W Sec 15, 1 (NMSU); 6.9 mi S, 2.0 mi E Bitter Creek, 7,000 ft, T17N R99W Sec 13, 1 (NMSU); 7.1 mi S, 0.9 mi E Bitter Creek, 7,100 ft, T17N R99W Sec 14, 1 (NMSU).

Thomomys idahoensis.—The only soft anatomical parts of phallic material of *T. idahoensis* examined in this study were from subadult individuals. Therefore, the following comments regarding the external phallus may be subject to some discrepancies due to age variation.

The phallus of *T. idahoensis* (Fig. 4) is long and slender, with a length eight to nine times greater than the width. The length of the glans is about half the length of the distal tract. The sides of the glans are somewhat expanded apically to the region of the urethral opening. Distal to the urethral opening a pair of long slender urethral processes are exposed. The protractile tip is relatively long compared to other species of *Thomomys*. In the subadult specimens examined there was no indication of a collar, midventral raphae, middorsal groove, or dorsal protuberances. Although epidermal structures were weakly-defined in specimens examined, *T. idahoensis* probably conforms to other members of the genus by having a single proximally oriented projection. It is possible that phallic features may become more prominent with maturity.

The length of the baculum among adults exam-

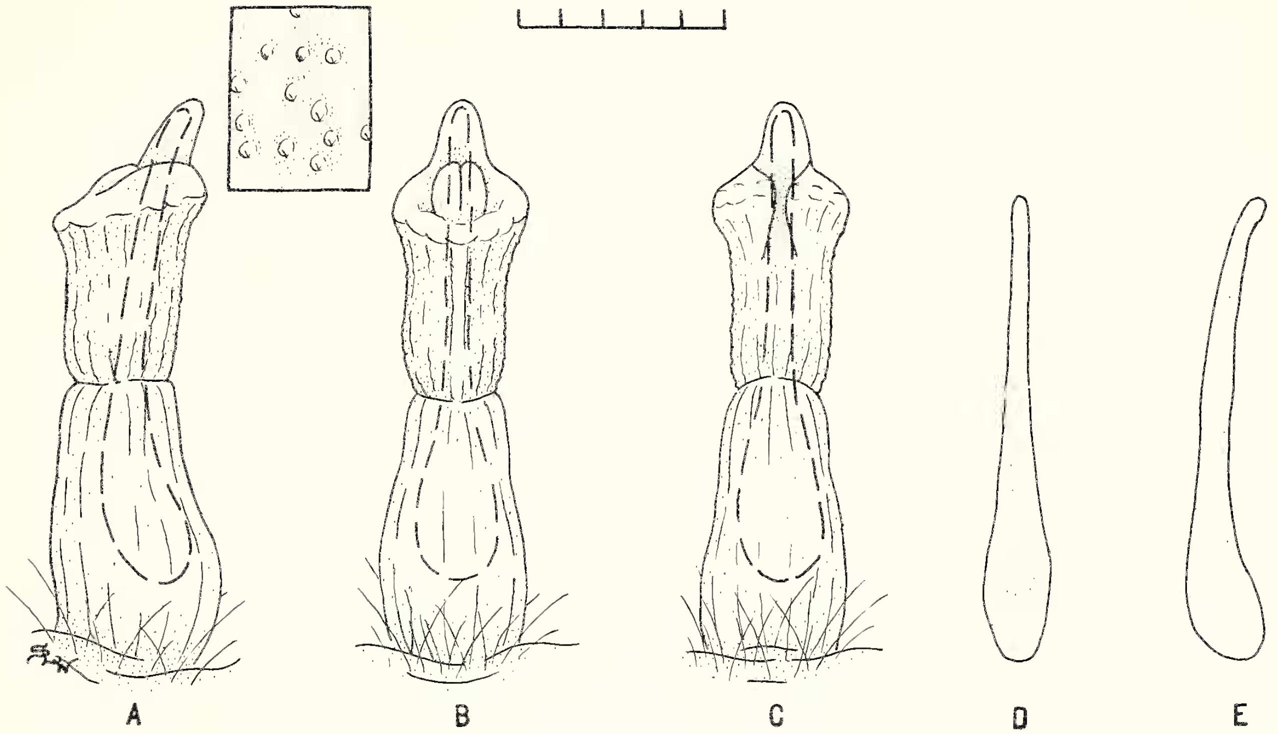

Fig. 3.—Phallus and baculum of *Thomomys clusius* from Wyoming: Carbon Co., 14.4 mi S, 6.0 mi E Rawlins (NMSU 5988), illustrated as in Fig. 1.

ined ranged from 16.2 to 23.4 mm. There were no consistent size relationships between height and width of the base. The baculum of *T. idahoensis* (Fig. 4) differs from previously discussed taxa by being relatively long, slender, and having a base and tip that are not as distinct. The ratio of the condylobasal length to the length of the baculum ranged from 1.4 to 1.7, except for the single specimen of *T. i. confinus* which had a ratio of 2.1. Observations of bacula of *T. idahoensis* in this study are in agreement with those of Long (1964) and Thaeler (1972).

Specimens examined.—Total (16).

T. i. confinus (1).—Montana: *Ravalli Co.:* 3.5 mi N, 6.0 mi E Stevensville, 3,650 ft, T9N R19W Sec 10, 1 (NMSU).

T. i. idahoensis (11).—Idaho: *Bingham Co.:* 0.5 mi N, 4.0 mi E Shelley, 4,670 ft, T1N R37E Sec 25, 1 (NMSU); *Bonneville Co.:* ½ mi N, 3½ mi W Idaho Falls, 5 (TTU); 5.3 mi N, 1.0 mi W Shelley, 4,650 ft, T2N R37E Sec 31, 1 (NMSU); 0.4 mi N, 1.0 mi W Swan Valley, 5,400 ft, T2N R43E Sec 35, 3 (NMSU); 0.6 mi S, 2.3 mi W Swan Valley, 5,400 ft, T1N R43E Sec 3, 1 (NMSU).

T. i. pygmaeus (4).—Wyoming: *Uinta Co.:* 0.8 mi N, 3.6 mi W Ft. Bridger, 7,000 ft, T16N R116W Sec 35, 4 (NMSU).

Thomomys mazama.—Like *T. idahoensis,* the phallus of *T. mazama* (Fig. 5) is considered long and slender. The distal tract of *T. mazama* is the longest of all geomyid species, with a length ranging from 27.2 to 34.1 mm among six adult specimens examined. The length is about 10 to 12 times greater than the width. The glans is between one-half and two-thirds the length of the distal tract. The sides of the glans are essentially straight and parallel. Similar to *T. idahoensis,* this species lacks many of the features found on other geomyid rodents. For instance, *T. mazama* does not possess a distinct collar, midventral raphae, or middorsal groove, and the constriction is not distinct. A dorsal protuberance may occur apically. The urethral processes are unique from other geomyid species in that they tend to be a continuation and a part of the ventral margin of the urethral opening. The protractile tip is shorter proportionally than that of *T. idahoensis.*

Epidermal structures are sparsely and erratically distributed from the urethral opening proximally for half the length of the glans. The structures, having single proximally oriented projections, are small, uniform in size, and have an irregular pattern.

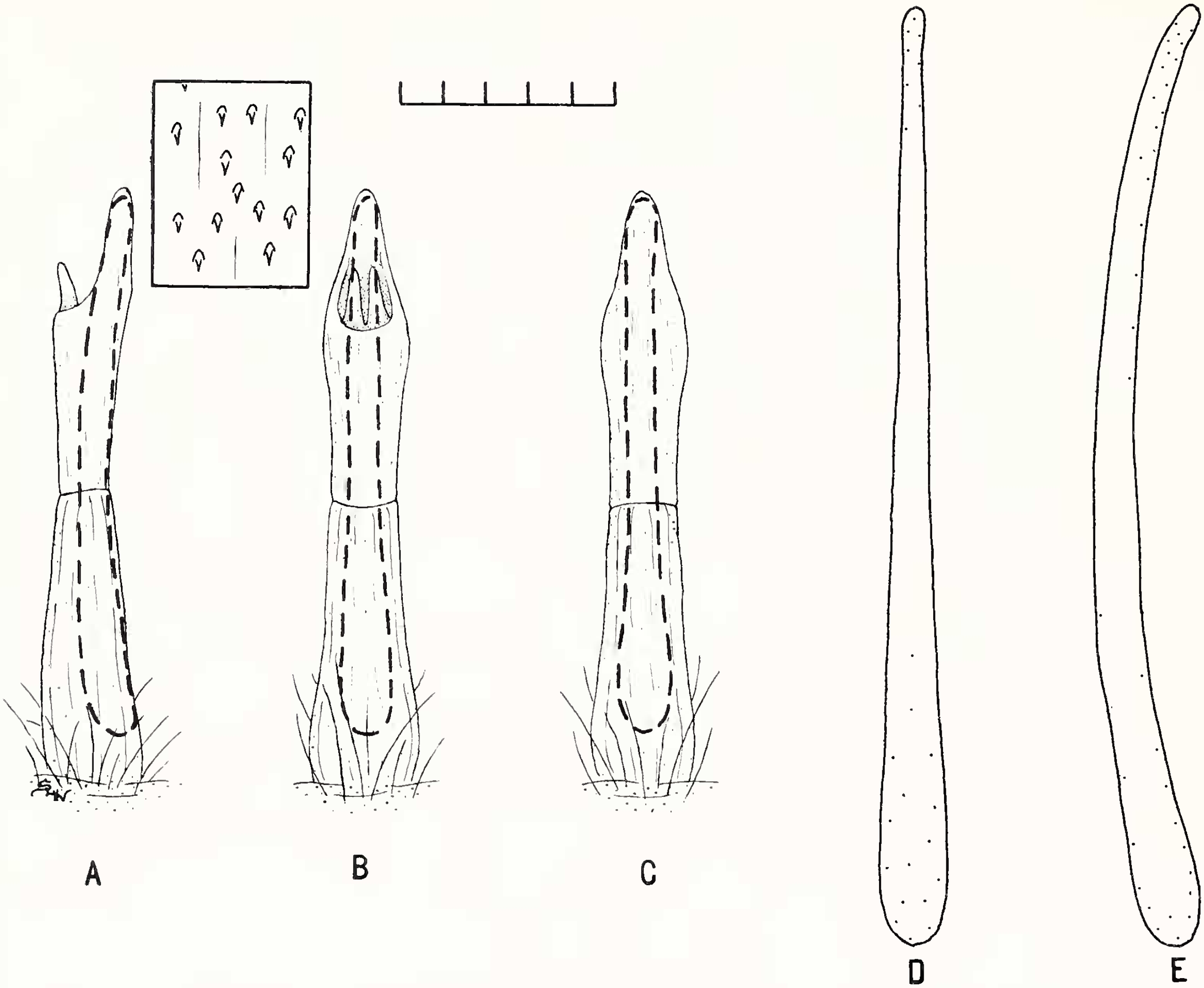

Fig. 4.—Phallus (A, B, C) of subadult *Thomomys idahoensis* from Idaho: Bonneville Co., ½ mi W Idaho Falls (TTU 19393), and baculum (D, E; same scale) of adult *T. idahoensis* from Idaho: Bonneville Co., 0.4 mi N, 1.0 mi W Swan Valley (NMSU 4812), illustrated as in Fig. 1.

Although the baculum of *T. mazama* (Fig. 5) resembles that of *T. idahoensis*, it differs by being larger and having a slightly more conspicuous base. Basically the baculum is long, slender, and has a weakly-defined tip and base. The length of the baculum among adult individuals examined ranged from 24.9 to 32.9 mm. Other investigators (Ingles, 1965; Johnson and Benson, 1960; Long and Frank, 1968; Thaeler, 1968) have placed the lower limits of bacular length at 21 and 22 mm. Although there is a tendency for the base of the baculum to be somewhat flattened dorsoventrally, the width of the baculum may equal or be slightly less than the height of the baculum base.

Thomomys mazama is unique from other geomyid species by having the longest distal tract and baculum, both absolutely and in proportion to the body size. An examination of six adult individuals showed a mean ratio of 1.2 with a range from 1.1 to 1.3, and a mean ratio of 1.3, with a range from 1.1 to 1.5, when comparing condylobasal length to length of distal tract and length of baculum, respectively. The ratio between the length of the distal tract and length of baculum averaged 1.0 and ranged from 1.0 to 1.2. (Every specimen had a distal tract that was longer than the baculum thus resulting in ratios greater than 1.0. Because the difference between both dimensions was often only detectable

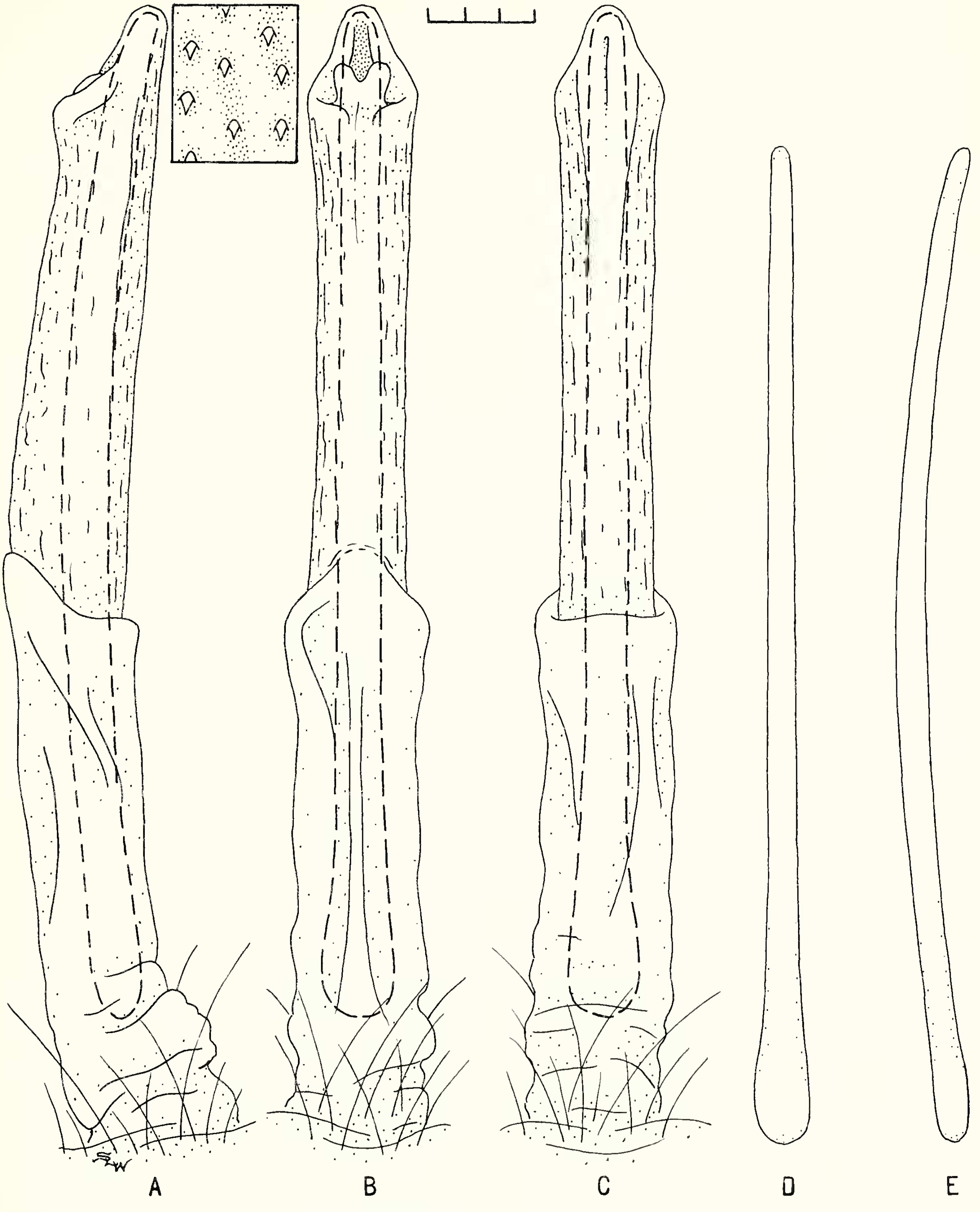

Fig. 5.—Phallus and baculum of *Thomomys mazama mazama* from California: Siskiyou Co., 3.6 mi S, 1.2 mi E Bartle, 4,250 ft (MVZ 129482), illustrated as in Fig. 1 (scale is three millimeters).

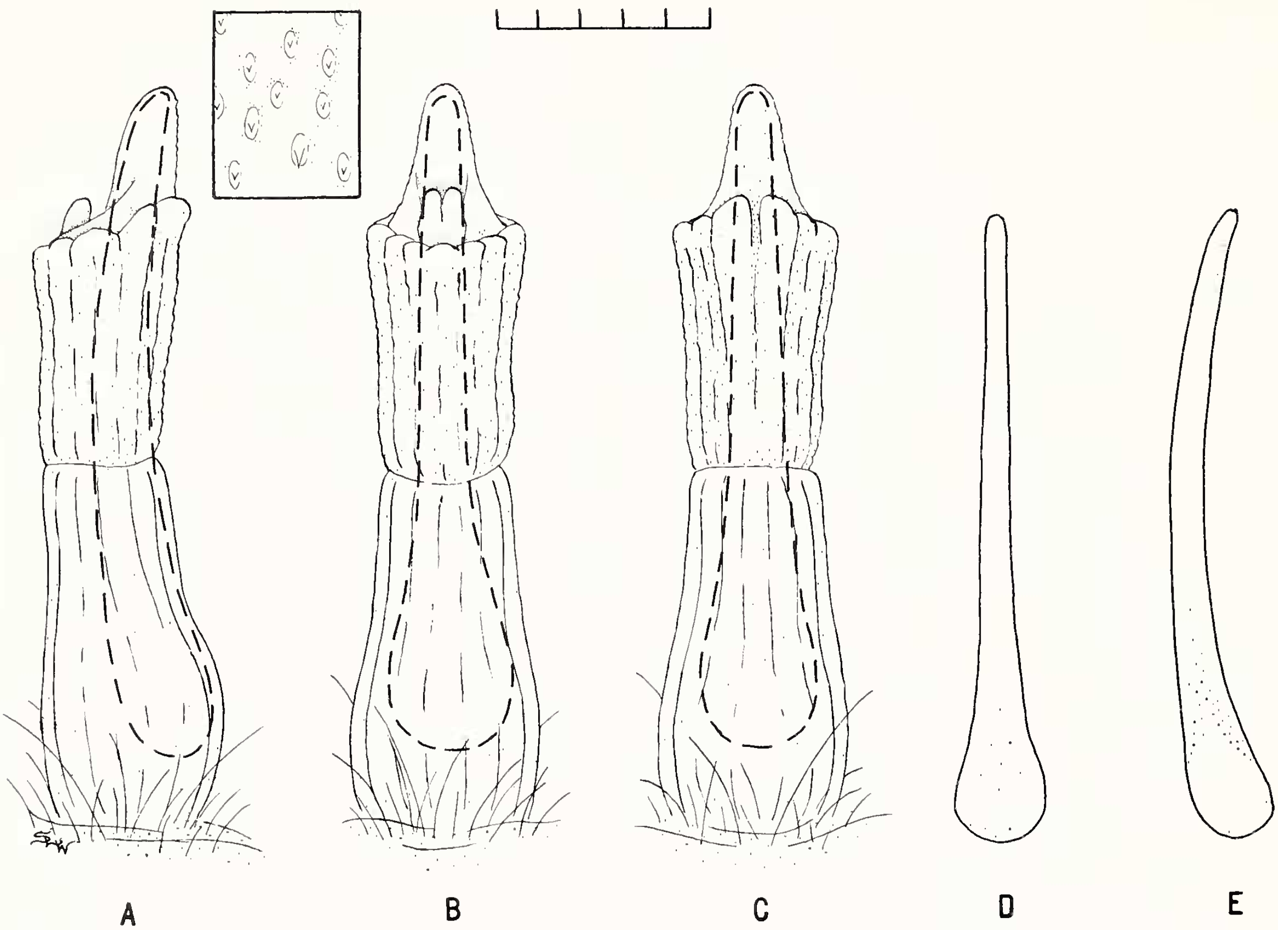

Fig. 6.—Phallus and baculum of *Thomomys monticola* from California: Siskiyou Co., ½ mi N Mount Shasta City, 3,600 ft (TTU 19407), illustrated as in Fig. 1.

beyond a single decimal position, procedures of rounding-off the ratio often resulted in a value of 1.0.)

Specimens examined.—Total (23).

T. m. mazama (23).—California: *Shasta Co.:* Dickson Flat, 4,200 ft, 4 (MVZ); Red Mountain, 5,400 ft, 1 (MVZ); *Siskiyou Co.:* Colby Meadow, 3.6 mi S, 1.2 mi E Bartle, 3 (MVZ); Lombardi Ranch, ¾ mi N, 1½ mi W Mount Shasta City, 3,525 ft, 3 (TTU); Lombardi Ranch, 1.5 mi WNW Mt. Shasta, 3,525 ft, 2 (MVZ); 1 mi W Mount Shasta City, 9 (CM). Oregon: *Jackson Co.:* 20 mi E Ashland, 1 (TTU).

Thomomys monticola.—The long and narrow-type phallus of *T. monticola* (Fig. 6) has a length six to seven times its width, with the length of the glans being about half the length of the distal tract. The length of the distal tract of nine adults examined ranged from 15.0 to 16.4 mm. From all aspects the sides of the glans are more or less straight and tend to expand apically. *Thomomys monticola* has a distinct collar that may be extended more distally on the dorsal side. A pair of well-developed urethral processes are exposed and may connect at the lower end of their common side. The midventral raphe, if present, is not distinct. *Thomomys monticola* possesses a middorsal groove and a pair of dorsal protuberances, but neither feature is well-developed. The constriction is well-defined.

Like other members of the genus *Thomomys*, the epidermal structures have a single proximally oriented projection. The structures are irregular in size, fairly uniform in pattern, and distributed between the collar and constriction and on the dorsal side of the protractile tip.

The baculum (Fig. 6) is distally tapered, possesses a distinct bulbous basal region, and is well curved. The length of the baculum of nine adults

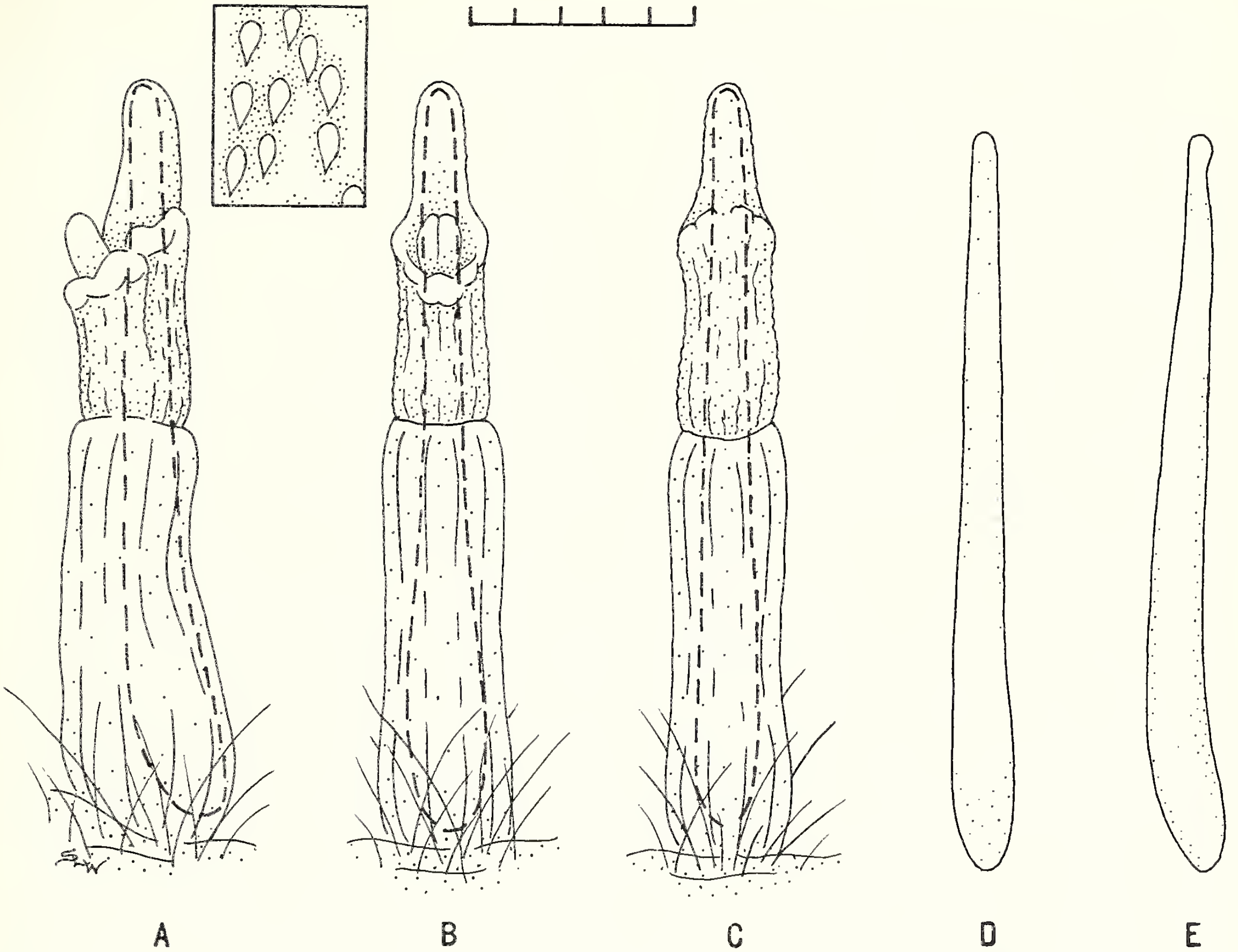

Fig. 7.—Phallus and baculum of *Thomomys talpoides fossor* from New Mexico: Taos Co., 1½ mi SE Taos Ski Area (TTU 9292), illustrated as in Fig. 1.

examined ranged from 13.8 to 15.2 mm. Descriptions and dimensions of the baculum of *T. monticola* closely agree with those of Long and Frank (1968) and Thaeler (1968). However, Ingles (1965) suggests the bacular length may range from 12 to 17 mm. There was no trend found between the width and height of the base of the baculum; the dimensions of one character may be greater than, less than, or equal to the other.

Among five adult individuals the ratio of the condylobasal length to the length of the distal tract and length of baculum averaged 2.2 (range, 2.1 to 2.3) and 2.4 (range, 2.3 to 2.5), respectively. In each case the ratio of the length of the distal tract to the length of the baculum was 1.1.

Specimens examined.—Total (15).

T. monticola (15).—California: *Madera Co.:* Agnew Meadow, 9.5 mi W Mammoth Lakes, 8,300 ft, 1 (MVZ); *Nevada Co.:* T17N R11E Sec 25, Bear Valley, 4,520 ft, 3 (MVZ); Sagehen Creek, 3 mi NW Hobart Mills, 6,400 ft, 5 (MVZ); Alder Creek, 4 mi NNE Truckee, 5,700 ft, 1 (MVZ); *Siskiyou Co.:* 3 mi S McCloud, 2 (TCWC); ½ mi N Mount Shasta City, 3,600 ft, 1 (TTU); Mount Shasta City, 2 (CM).

Thomomys talpoides.—The phallus of *T. talpoides* (Fig. 7) is considered to be long and narrow like that of *T. idahoensis*, *T. mazama*, and *T. monticola* although its size is quite variable compared to other species of *Thomomys*. The distal tract in *T. talpoides* is about eight to nine times longer than its width. The length of the glans is less than half the length of the distal tract which ranges from 14.0 to 26.2 mm among adult specimens examined. The phallus of *T. talpoides* more closely resembles that of *T. monticola* than any other species of *Thomomys* because of its similar size, shape, and features. The sides of the glans are essentially parallel but curve toward the dorsal side to conform with the shape of the baculum. In the region of the collar, the sides expand slightly. The glans of *T. talpoides* is basically featureless by lacking a well-developed midventral raphe, middorsal groove, and dorsal protuberances. However, the collar and constriction of *T. talpoides* tend to be somewhat more distinct. The urethral processes are long and narrow.

The epidermal structures have a single proximally oriented projection and are relatively small and uniform in size and pattern. The epidermal structures are distributed between the collar region and the constriction.

The baculum (Fig. 7) of *T. talpoides,* which is also variable within the species, consists primarily of a simple, slightly curved shaft with the tip and base being barely discernable. The height and width of the bacular base may be greater than, less than, or equal to the other. The length of the baculum among adult specimens examined ranged from 12.3 to 22.6 mm. Data presented by other investigators (Burt, 1960; Ingles, 1965; Johnson and Benson, 1960; Long, 1964; Long and Frank, 1968; Thaeler, 1968) indicate considerable variation of bacula among geographical races of *T. talpoides,* with bacular lengths ranging from 10.4 to 31.0 mm. Although variation occurs within the species, data presented in this study, combined with data from other published sources, indicate broad geographical trends in baculum sizes. For instance, subspecies reported having smaller bacula tend to be clustered on the western part of the range, whereas the races reported to have larger bacula occur primarily in the eastern half of the range.

The ratios of the condylobasal length to the length of the distal tract and length of baculum ranged from 1.4 to 2.5 and 1.6 to 2.9, respectively. The ratio between the length of the distal tract and length of baculum ranged from 1.0 to 1.1.

Specimens examined.—Total (35).

T. t. bridgeri (16).—IDAHO: *Bear Lake Co.:* Home Canyon, 5 mi NE Montepelier, 1 (TCWC); ½ mi S, 4¼ mi E Palisades, 6,400 ft 15 (CM).

T. t. bullatus (3).—MONTANA: *Custer Co.:* 10 mi S, 3 mi E Locate, 3 (CM).

T. t. devexus (1).—WASHINGTON: *Grant Co.:* 5 mi N Coulee City, 1,600 m, 1 (TCWC).

T. t. fossor (3).—COLORADO: *Chaffee Co.:* Trout Creek, 8½ mi NE Buena Vista, 1 (TCWC). NEW MEXICO: *Taos Co.:* 1½ mi SE Taos ski area, 1 (TTU); beaver pond SE Taos ski area, 1 (TTU).

T. t. fuscus (1).—IDAHO: *Blaine Co.:* Alturas Lake, 7,000 ft, 1 (TCWC).

T. t. quadratus (3).—IDAHO: *Owyhee Co.:* 12 mi S, 7 mi W Murphy, 3 (CM).

T. t. rostralis (2).—WYOMING: *Albany Co.:* 5 mi N Laramie, 1 (TTU); 3.5 mi N Laramie, 1 (TTU).

T. t. rufescens (3).—MANITOBA: 11 mi E Dauphin, 1 (TCWC). NORTH DAKOTA: *Morton Co.:* 8 mi S, 15 mi W Mandan, 1 (CM); *Williams Co.:* 1 mi N Buford, 2,100 ft, 1 (CM).

T. t. saturatus (1).—IDAHO: *Bonner Co.:* 2½ mi N Nordman, 2,700 ft, 1 (TCWC).

T. t. talpoides (1).—SASKATCHEWAN: 13 mi S Blaine Lake, 1,600 ft, 1 (TCWC).

T. t. tenellus (1).—COLORADO: *Rio Blanco Co.:* 22 mi SW Meeker, 6,200 ft, 1 (TCWC).

Thomomys townsendii.—The shape and features of the phallus of *T. townsendii* (Fig. 8) are most similar to *T. bottae* and *T. umbrinus* with the primary difference being a larger size in *T. townsendii.* The length of the distal tract, which ranged from 13.0 to 15.5 mm among adult specimens examined, is four to five times greater than the width. The length of the glans is about half the length of the distal tract. The sides of the glans expand to the collar and are recurved. The collar is distinct from all aspects. The pair of urethral processes are exposed and well-developed. Standard features, including the midventral raphae, middorsal groove, dorsal protuberances, and distinct constriction, are present. All of these features, except perhaps the dorsal protuberances, are well defined. The middorsal groove extends from about the middle of the protractile tip to about halfway between the collar and constriction.

The epidermal structures have single, relatively large, proximally oriented projections. The pattern and size is fairly uniform. The structures occur between the collar and constriction and on the dorsal side of the protractile tip.

The baculum of *T. townsendii* (Fig. 8) is strongly curved with the dorsal side being concave as in other geomyid bacula. The baculum has a distinct tip and bulbous base. The length of the baculum ranged from 12.2 to 13.9 mm among adult individuals examined. Ingles (1965) and Thaeler (1968) reported bacular lengths of *T. townsendii* to be as short as 9.2 mm and 10.7 mm, respectively. In adult specimens of *T. t. bachmani* and *T. t. similis* examined,

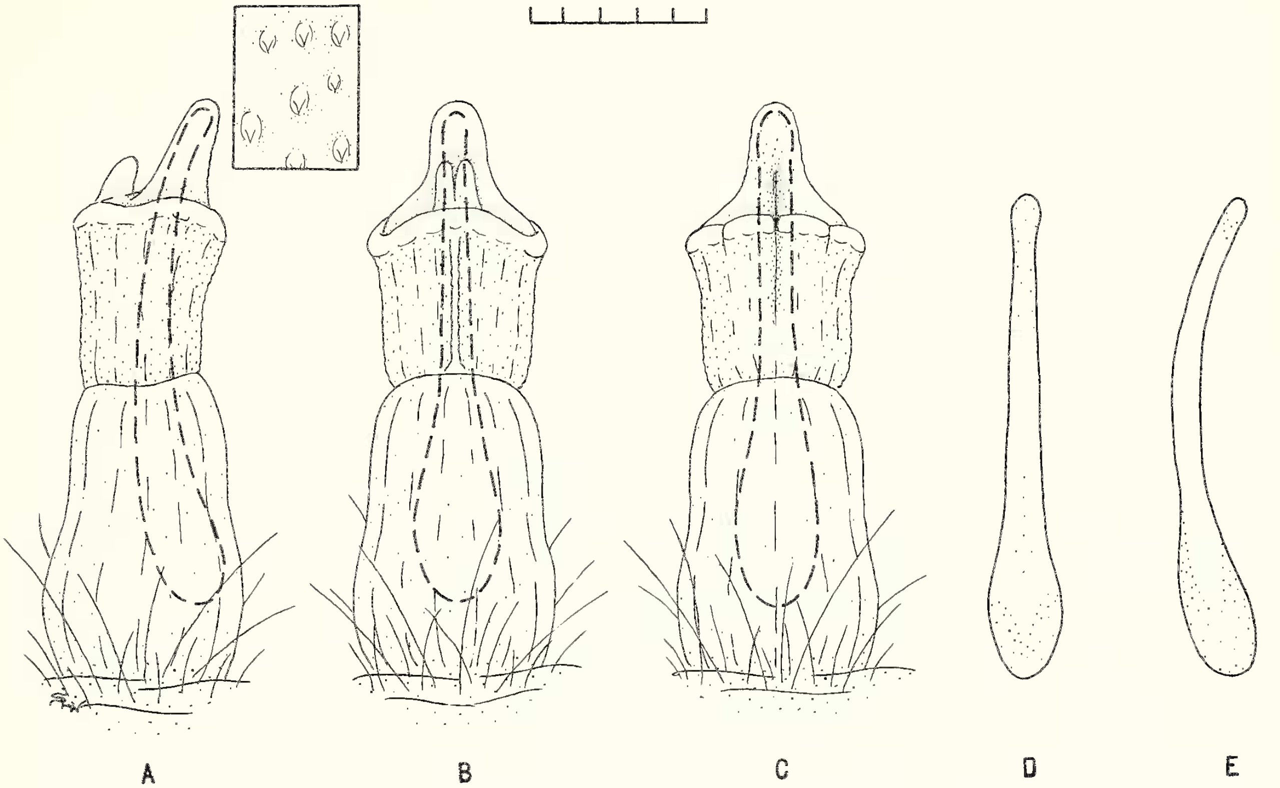

Fig. 8.—Phallus and baculum of *Thomomys townsendii townsendii* from Idaho: Canyon Co., 1 mi N Caldwell (TTU 19420), illustrated as in Fig. 1.

the width of the baculum base was always less than the height of the base; the opposite was found in *T. t. townsendii*.

The ratios of condylobasal length to the length of the distal tract ranged from 3.1 to 3.6; condylobasal length to length of baculum ranged from 3.6 to 3.9; length of the distal tract to the length of the baculum was 1.1 in all cases.

Specimens examined.—Total (9)

T. t. bachmani (2).—OREGON: *Harney Co.:* Harney Lake Dunes, Malheur National Wildlife Refuge, T26S R30E Sec 28, 2 (CM).
T. t. similis (3).—IDAHO: *Bingham Co.:* 2½ mi S Springfield, 4,400 ft, 3 (CM).
T. t. townsendii (4).—IDAHO: *Canyon Co.:* 1 mi N Caldwell, 4 (TTU).

Thomomys umbrinus.—The shape and size of the phallus of *T. umbrinus* (Fig. 9) is most similar to *T. bottae*. Because the available material for both *T. bottae* and *T. umbrinus* is restricted to limited areas of the extensive geographic ranges of both species, further study of geographic and nongeographic variation is needed before specific differences can be defined.

The length of the phallus of *T. umbrinus* is about four times greater than the width. The glans is about half the length of the distal tract. The length of the distal tract ranged from 10.3 to 12.3 mm among adult individuals examined. Viewed dorsoventrally, the sides of the glans may be straight or recurved but tend to be more or less parallel. The collar region is expanded and distinct. The urethral processes are well developed but connected for most of the length along the common side. Other features noted include a well-defined midventral raphe, poorly-developed middorsal groove, and the absence of dorsal protuberances.

The epidermal structures of *T. umbrinus* have the characteristic single, proximally oriented projection, common to other members of the genus. The structures are relatively large and uniform in size and pattern.

The baculum of *T. umbrinus* (Fig. 9) is similar to that of *T. bottae* but tends to be shorter. A definite

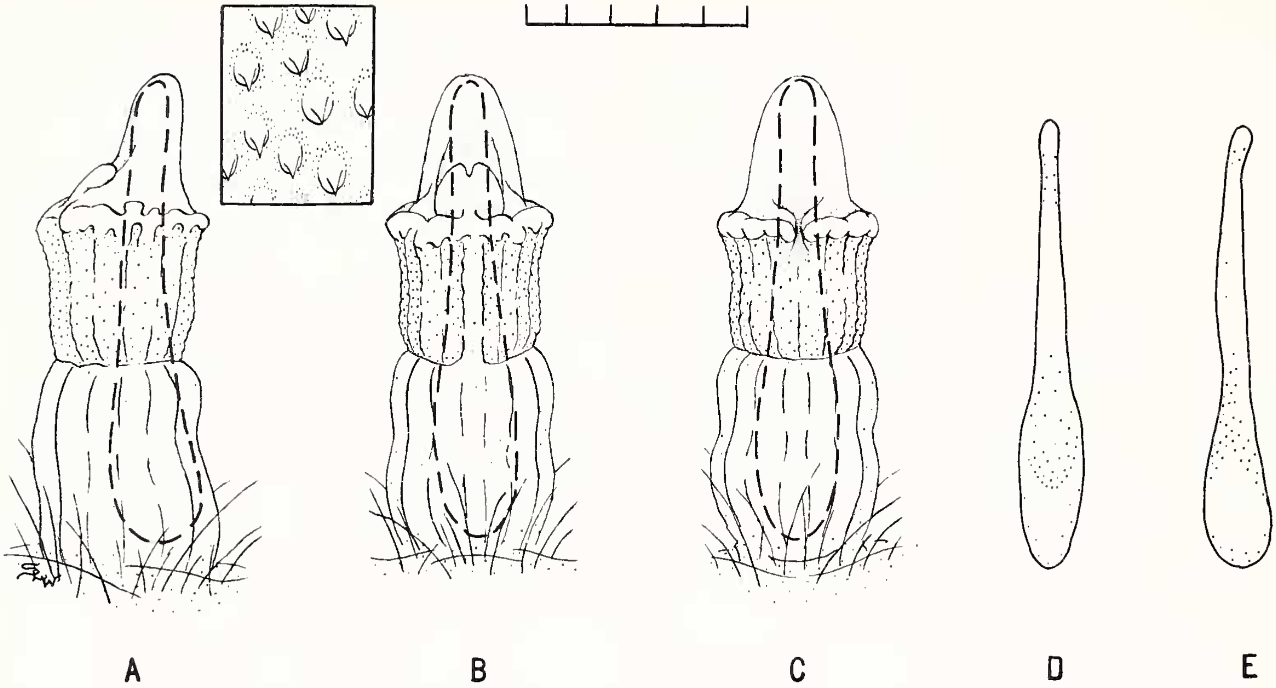

Fig. 9.—Phallus and baculum of *Thomomys umbrinus* from Tlaxcala: La Malinche Mt., 8 km S, 7 km W Huamantla (CM 55893), illustrated as in Fig. 1.

base and tip are present; the shaft is curved. The length of the baculum ranged from 8.0 to 11.3 mm among adult specimens examined. In most individuals examined the width and height of the base of the baculum were very close to being equal. Like *T. bottae* and *T. talpoides,* the baculum of *T. umbrinus* demonstrates geographical variability. Bacula from Arizona reported by Burt (1960), Hoffmeister (1969), and Patton (1973) were smaller (9.0 to 10.2 mm), had a bulbous base, and had a well curved shaft. Data presented here suggest these characters are variable when other subspecies, throughout the range of *T. umbrinus,* are considered.

The ratios of condylobasal length to the length of the distal tract and length of the baculum ranged from 3.2 to 3.7 and 3.6 to 4.5, respectively. The ratio between the length of the distal tract and the length of the baculum ranged from 1.0 to 1.3.

Specimens examined.—Total (28).

T. u. arriagensis (1).—San Luis Potosi: 4 mi E Villa Arriaga, 1 (MVZ).

T. u. intermedius (8).—Arizona: *Santa Cruz Co.:* Gardner Canyon, 3.0 mi N, 3.7 mi W Sonoita, 3 (TTU); Patagonia Mts., Italian Canyon 1 (MVZ); Patagonia Mts., Sycamore Canyon, 4,500 ft, 4 (MVZ).

T. u. juntae (1).—Chihuahua: 1 mi S Delicias, 1 (TTU).

T. u. madrensis (2).—Chihuahua: 2.4 mi NE Colonia Garcia, 1 (MVZ); 1 mi W Colonia Garcia, 1 (MVZ).

T. u. sheldoni (4).—Durango: 3 mi NW El Salto, 4 (MVZ).

T. u. ssp. (12).—Tlaxcala: 10 km N, 9 km E Apizaco, 2,500 m, 1 (CM); 9 km N, 7 km E Apizaco, 2,500 m, 3 (CM); 8 km S, 7 km W Calpulalpan, 2,900 m, 4 (CM); La Malinche Mt., 7 km S, 11 km W Huamantla, 4,800 m, 1 (CM); La Malinche Mt., 8 km S, 7 km W Huamantla, 4,000 m, 2 (CM); 4 km N, 19 km W Tlaxcala, 2,200 m, 1 (CM).

Statistics

Age variation in phallic characters of *Thomomys* was observed in this study and has been reported by other investigators (Burt, 1960; Johnson and Benson, 1960). However, proper analysis and documentation of this form of variation is beyond the scope of the present study. Table 1 provides standard statistics (sample size, mean, range, standard error, and coefficient of variation) for adult specimens of *Thomomys* examined.

Examination of individual variation was conducted on four species of *Thomomys,* thus providing a general assessment of the individual variation in the genus. Each sample included individuals taken from a restricted geographical area that would be assumed to be part of a continuous population.

The taxa examined for individual variation were *T. bottae opulentus*, *T. bulbivorous*, *T. mazama mazama*, and *T. talpoides bridgeri*. Coefficients of variation in these samples ranged from 1.0 to 25.4 for phallic and bacular measurements, with the above taxa averaging 14.3, 11.4, 15.0, and 9.2, respectively. Generally, the length of the distal tract and the length of the baculum had the lowest values, and the length of the protractile tip and the width of the glans at the collar had the highest values. The characters having the lowest and highest coefficients of variation for *T. bottae* were length of distal tract (1.0) and width of glans across the base (24.8); for *T. bulbivorous*, length of baculum (2.9) and length of protractile tip (22.0); for *T. mazama*, length of glans (7.6) and length of protractile tip (25.4); for *T. talpoides*, length of distal tract (3.9) and length of protractile tip (14.1). Compared to investigations of the baculum by Long and Frank (1968) coefficients of variation acquired in this study (Table 1) were high for *T. mazama* and *T. monticola*, low for *T. townsendii*, and overlapping in *T. bottae* and *T. talpoides*.

Sample sizes and limited geographical coverage of specimens representing species of *Thomomys* precludes any meaningful analysis of geographic variation within a species from being conducted. However, examination and comparison of measurements of individuals strongly suggests that variation, at least in size, does occur between geographical races, or subspecies, of *Thomomys*. In four out of eight characters *T. bottae* and *T. umbrinus* had subspecies with nonoverlapping measurements. *Thomomys talpoides* and *T. townsendii* had subspecies that did not overlap in five and six characters, respectively. The greatest variation between geographical races was observed in *T. talpoides*.

Examination of variation among species of *Thomomys* was restricted to multivariate analysis, using sample means with the MINT statistical computer program. Univariate analysis was not used because the sample sizes of most geographical races were limited, and combining samples of the same species could lead to a biased representation of the species, particularly if geographic variation occurs within the species. The samples of *Thomomys* used in the multivariate analysis, with corresponding number for reference purposes, are six subspecies of *T. bottae* (*actuosus*, 1; *connectens*, 2; *limitaris*, 3; *limpiae*, 4; *opulentus*, 5; *ruidosae*, 6), *T. bulbivorous* (7), *T. clusius* (8), *T. mazama mazama* (9), *T. monticola* (10), ten subspecies of *T. talpoides* (*bridgeri*, 11; *fossor*, 12; *fuscus*, 13; *quadratus*, 14; *rostralis*, 15; *rufescens*, 16; *saturatus*, 17; *talpoides*, 18; *tenellus*, 19), three subspecies of *T. townsendii* (*bachmani*, 20; *similis*, 21; *townsendii*, 22), and four subspecies of *T. umbrinus* (*intermedius*, 23; *juntae*, 24; *sheldoni*, 25; ssp. from Tlaxcala, 26).

The distance phenogram produced by the MINT program is illustrated in Fig. 10. The cophenetic correlation value of this phenogram was 0.820. Although clustering of samples shows mixing between species, some trends are evident. *T. mazama* formed a group distinct from all other taxa. The next two groups to split away from the remaining samples were *T. bulbivorous* and *T. u. juntae* which clustered together but remained distinct from each other. The next subdivisions isolate *T. u. intermedius* and then break down into two large clusters. One cluster consists of seven subspecies of *T. talpoides* (*bridgeri*, *rufescens*, *fossor*, *saturatus*, *talpoides*, *tenellus*, and *rostralis*). The second cluster subdivides to form a cluster consisting of the three subspecies of *T. townsendii* (*similis*, *bachmani*, and *townsendii*) and *T. b. connectens*. The other cluster consists of a mosaic of taxonomic groups. In the remaining clusters *T. b. actuosus*, *T. b. opulentus*, *T. b. ruidosae*, and *T. t. fuscus* form one group; *T. b. limitaris*, *T. monticola*, *T. t. quadratus*, *T. b. limpiae*, and *T. clusius* form one group; *T. u. sheldoni* and *T. umbrinus* from Tlaxcala form the final group.

The first three principal components extracted from the matrix of correlation among characters is illustrated in Fig. 11. The first vector separates three general groups. The first group consists of *T. mazama* (9) which is plotted to the far left. The second grouping includes *T. monticola* (10) and the samples of *T. talpoides* (11–19). In the second grouping the westernmost subspecies of *T. talpoides*, represented by *T. t. fuscus* and *T. t. quadratus*, cluster together on the right side of the group with *T. monticola*. *T. monticola* falls within the range of *T. talpoides* with all three vectors. The third group consists of the samples of *T. bottae* (1–6), *T. bulbivorous* (7), *T. clusius* (8), *T. townsendii* (20–22), and *T. umbrinus* (23–26). In the third group *T. bottae* and *T. clusius* are separated from *T. bulbivorous* and *T. umbrinus* with the first vector. *T. bulbivorous* and *T. clusius* are separated with the second and third vectors, respectively. *T. townsendii* overlaps with *T. bottae* and *T. umbrinus* with all three vectors.

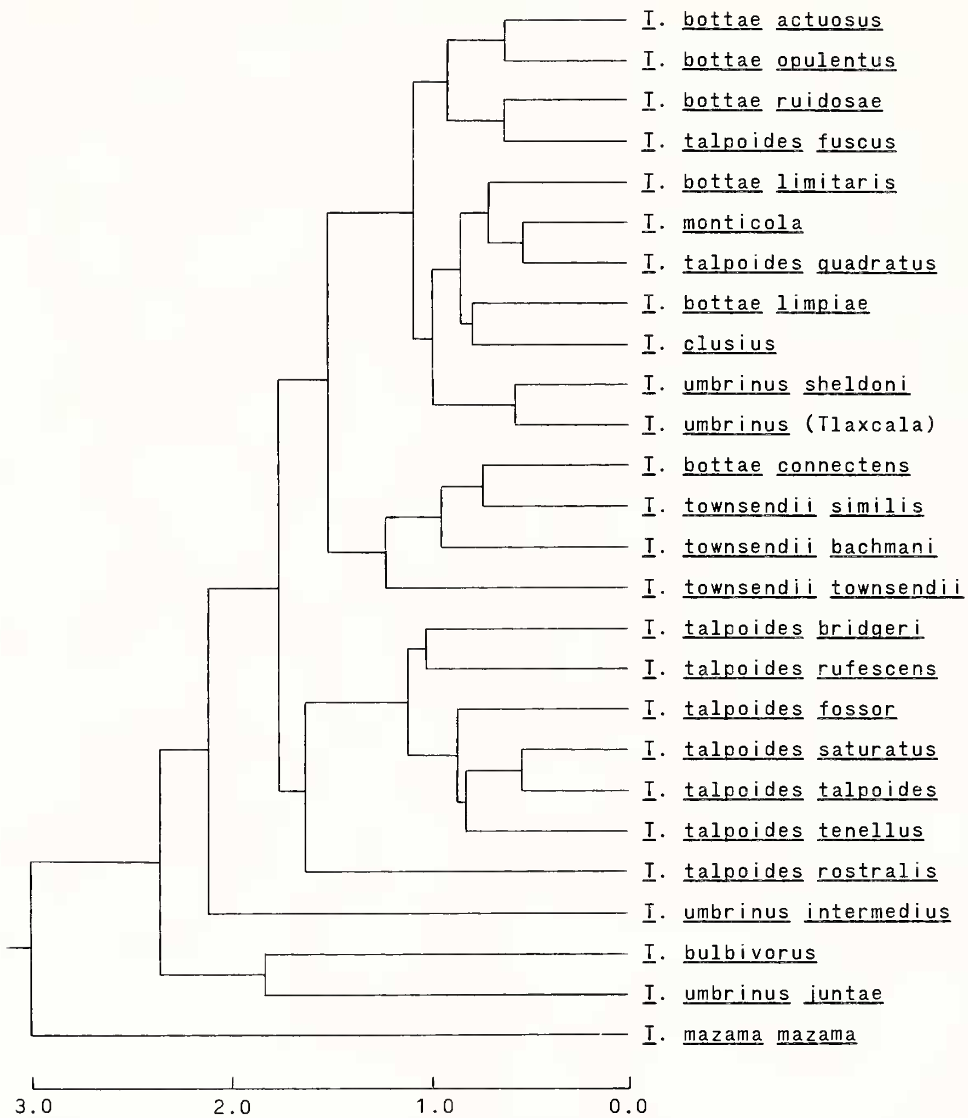

Fig. 10.—Distance phenogram of 26 samples of *Thomomys* resulting from clustering by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.820.

The amount of phenetic variation explained by components I, II, and III, is 39.2%, 31.7%, and 11.1%, respectively. Results of principal component analyses, showing the influence of each character for the first three components, are given in Table 2. For component I the length of the distal tract, length of glans, and the length of the baculum are the most heavily weighted. The width of the glans across the base, width of bacular base, and height of bacular base are the most heavily weighted characters in component II. For component III the length of the protractile tip is the most heavily weighted character.

Orthogeomys

Description

Orthogeomys hispidus.—In this study the genus *Orthogeomys* is only represented by samples of *O. hispidus*. The length of the phallus of *O. hispidus* (Fig. 12) is about four times longer than the width, with the length of the glans being slightly more than half the length of the distal tract. The length of the distal tract of two adult specimens examined was

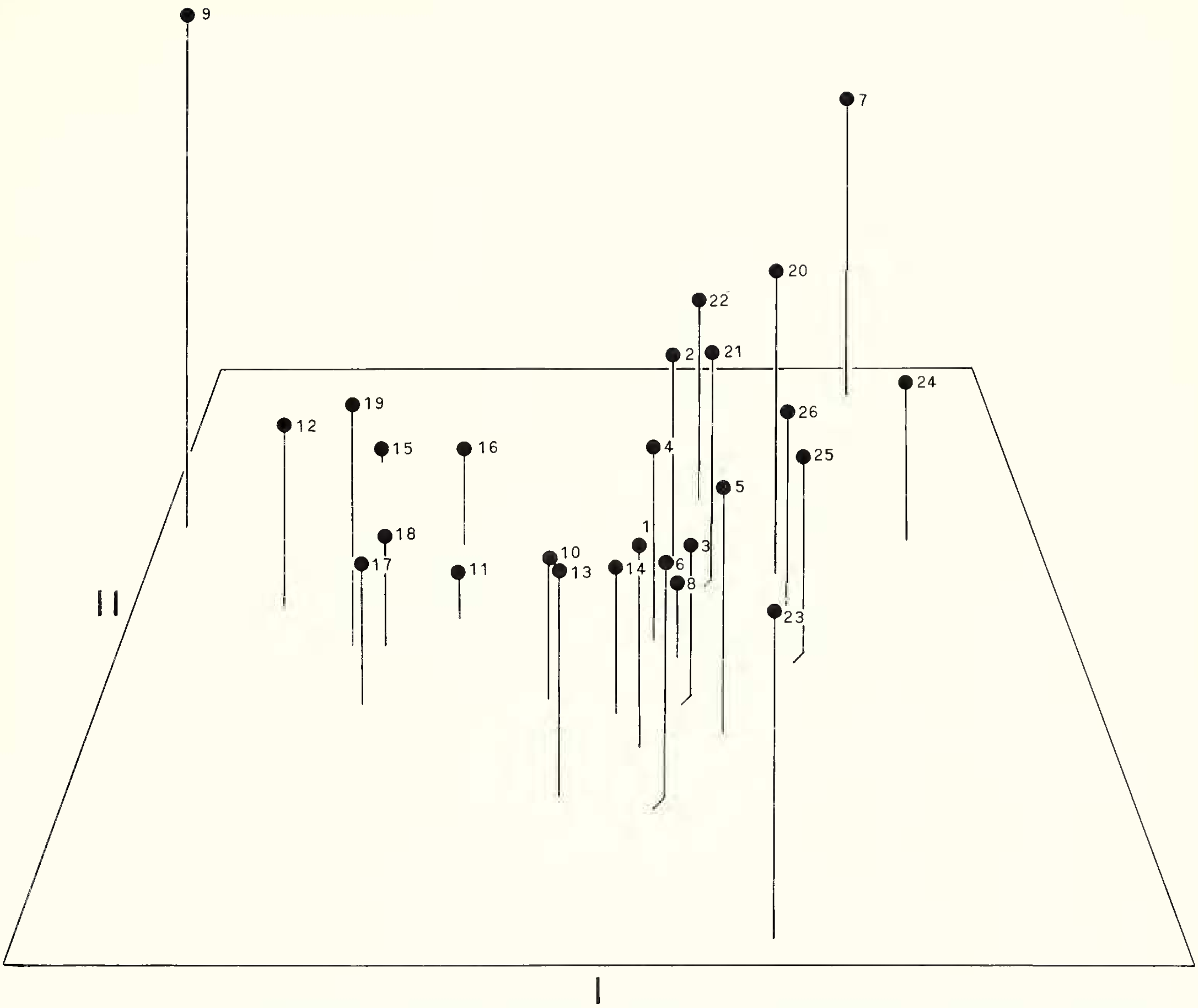

Fig. 11.—Three-dimensional projection of 26 samples of *Thomomys* (*T. bottae*, 1–6; *T. bulbivorous*, 7; *T. clusius*, 8; *T. mazama*, 9; *T. monticola*, 10; *T. talpoides*, 11–19; *T. townsendii*, 20–22; *T. umbrinus*, 23–26) onto the first three principal components based upon a matrix of correlation among one cranial, five phallic, and three bacular measurements. Components I and II are indicated in the plots and component III is represented by height.

15.5 and 15.7 mm. The sides of the glans, from all aspects, are more or less straight and parallel, and expanded slightly at the collar. The collar is distinct on all sides except in the middorsal region. On the dorsal side the collar is extended more distally than on the other sides. The urethral processes are small and partially concealed by the collar. The midventral raphe is well-developed. The dorsal side is featured with a single prominant protuberance which may have a shallow middorsal depression that constitutes the middorsal groove found in other geomyid species. The dorsal protuberance is evident from the protractile tip to the lower portion of the glans where it fades out.

The epidermal structures of *O. hispidus* are large and consist of a single (occasionally two) proximally oriented projection. The size and pattern of the epidermal structures is fairly uniform. The structures are restricted to the area between the constriction and collar.

The baculum of *O. hispidus* (Fig. 12) is massive compared to bacula of most other geomyid rodents. The base is somewhat bulbous and compressed dorsoventrally. The base gradually tapers to the thick

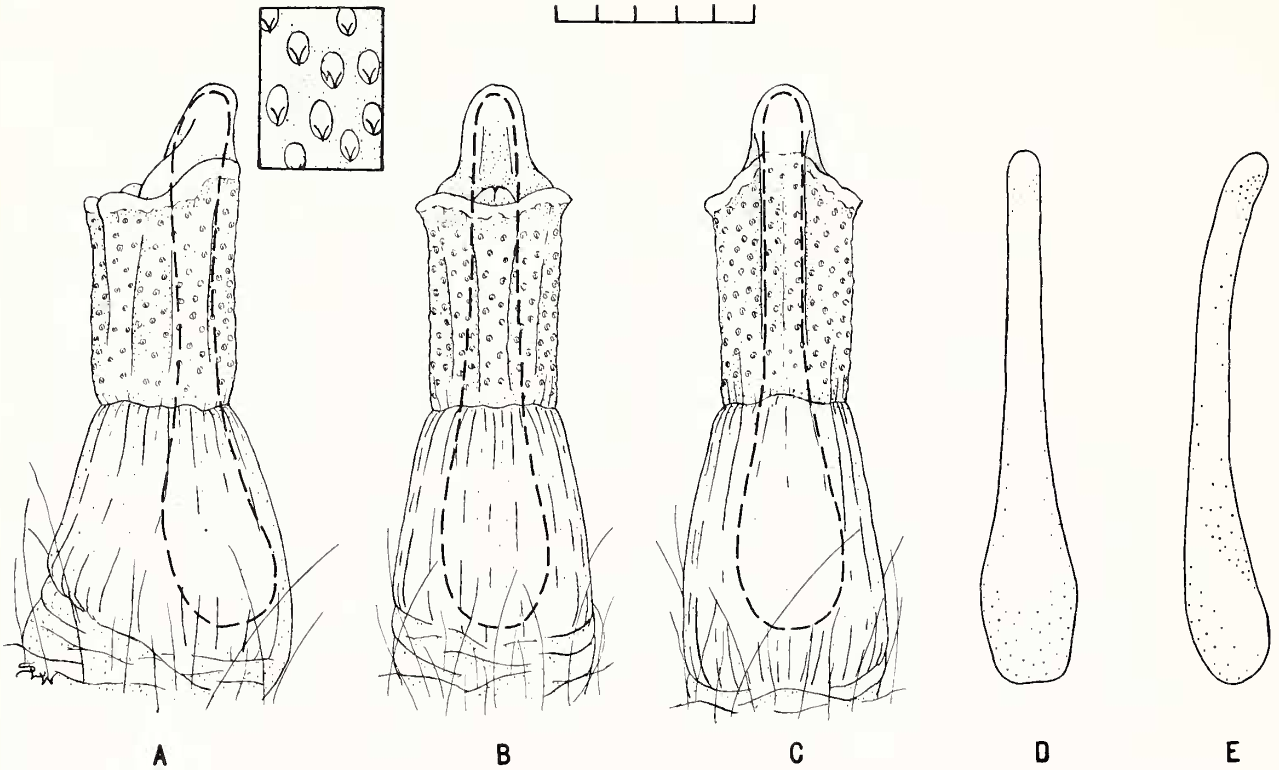

Fig. 12.—Phallus and baculum of *Orthogeomys hispidus negatus* from Tamaulipas: 67 km S Ciudad Victoria (CM 55787), illustrated as in Fig. 1.

shaft which terminates with a weakly defined tip. The entire baculum is well-curved. The length of the baculum of two adult specimens examined was 12.8 and 13.7 mm.

For two adult specimens, the ratios of the condylobasal length to the length of the distal tract were 3.9 and 4.1; ratios of the condylobasal length to the length of baculum were 4.7 and 4.8; ratios of the length of the distal tract to the length of baculum were 1.1 and 1.2.

Samples of *O. hispidus* are inadequate for statistical analyses. Table 3 provides measurements of specimens of *O. hispidus* examined in this study.

Table 2.—*Factor matrix from correlation among nine characters of eight species (26 samples of* Thomomys *examined.*

Character	Component I	Component II	Component III
Condylobasal length	0.469	−0.547	0.287
Length of distal tract	−0.930	−0.300	0.180
Length of glans	−0.878	−0.341	0.289
Length of protractile tip	−0.544	−0.308	−0.681
Width of glans across collar	0.577	−0.622	−0.043
Width of glans across base	0.279	−0.789	0.389
Length of baculum	−0.933	−0.293	0.139
Width of bacular base	−0.045	−0.790	−0.362
Height of bacular base	0.300	−0.729	−0.185

Specimens examined.—Total (8).

O. h. chiapensis (1).—Chiapas: 7.5 mi (by road) NW Pueblo Nuevo, 6,000 ft, 1 (KU).

O. h. isthmicus (1).—Veracruz: 5 mi SE Lerdo de Tejada, 1 (KU).

O. h. negatus (4).—Tamaulipas: 45 mi S Cd. Victoria, 2 (TTU); 67 km S Cd. Victoria, 2 (1 CM, 1 TTU).

O. h. torridus (1).—Veracruz: 12½ mi N Tihuatlan, 300 ft, 1 (KU).

O. h. yucatanensis (1).—Quintana Roo: 6.5 km NE Playa del Carmen, 1 (TTU).

Zygogeomys

Description

Zygogeomys trichopus.—In this study the phallus of *Zygogeomys* (Fig. 13) is represented by a juvenile and a young adult specimen. Because the basioccipital and basisphenoid are not well fused in the young adult specimen, the following comments based on that single specimen may be subject to some discrepancies due to age variation. Measurements for the specimen are given in Table 3.

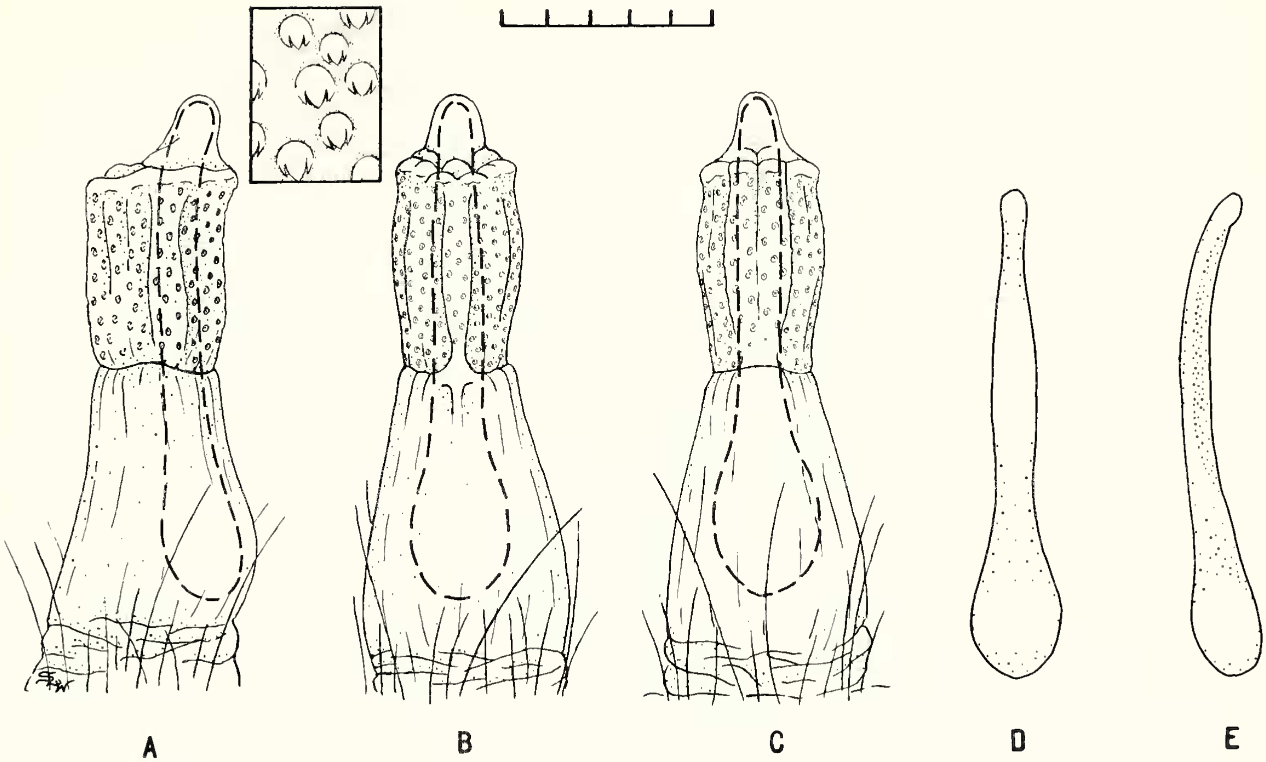

Fig. 13.—Phallus and baculum of *Zygogeomys trichopus trichopus* from Michoacan: 5.3 km E Tacitaro (CM 55902), illustrated as in Fig. 1.

The distal tract is four to five times longer than wide, and measures 14.7 mm. The glans is less than half the length of the distal tract and is somewhat narrower when viewed dorsoventrally than when viewed from a lateral aspect. From a lateral aspect the ventral side is straight, whereas the dorsal side is recurved with the widest part being the collar. Viewed dorsoventrally the lateral sides show a bulge in the midsection of the glans and a slight expansion at the collar. The collar is distinct from all aspects. The pair of urethral processes and the protractile tip are reduced in size compared to other members of the family. The urethral processes are almost hidden by the collar. Other features include a well-defined constriction, prominent midventral raphe, a middorsal groove, and a pair of well-developed dorsal protuberances. The middorsal groove in this specimen begins at the lower portion

Table 3.—*Dimensions of external phallic characters, bacular characters, condylobasal length, and hind foot length of individuals of* Orthogeomys *and* Zygogeomys *examined. Young adult specimens had well-developed sagittal and lambdoidal crests and lacked complete fusion between the basioccipital and basisphenoid.*

Taxon	Catalog number	Age	Length of distal tract	Length of glans	Length of protractile tip	Width of glans across collar	Width of glans across base	Length of baculum	Width of bacular base	Height of bacular base	Condylobasal length	Length of hind foot
Orthogeomys hispidus isthmicus	KU 67625	Young Adult	16.5	9.4	3.5	—	—	14.6	2.5	1.3	62.6	52
Orthogeomys hispidus negatus	CM 55787	Adult	15.5	8.7	3.5	5.0	3.4	13.7	2.7	2.0	63.9	49
Orthogeomys hispidus negatus	TTU 10248	Adult	15.7	—	—	—	—	12.8	2.1	1.5	61.9	41
Orthogeomys hispidus negatus	TTU 14339	Young Adult	14.8	7.5	2.9	3.6	3.5	11.7	1.9	1.3	54.7	39
Orthogeomys hispidus torridus	KU 88521	Young Adult	15.7	7.9	2.7	—	—	13.1	2.7	1.3	61.3	46
Zygogeomys trichopus trichopus	CM 55902	Young Adult	14.7	7.0	2.1	3.3	2.9	12.7	2.4	1.7	58.3	46

of the protractile tip, crosses the collar and continues for half the length of the glans where it fades out. The dorsal protuberances are more or less distinct for the entire distance between the collar and constriction.

The epidermal structures are large and disk-shaped with three proximally oriented projections lying side-by-side. The epidermal structures are somewhat variable in size and may be restricted to the region of the glans between the collar and constriction.

The baculum of the specimen examined (Fig. 13) is 12.7 mm in length and has a distinct base and tip. The shaft is constricted on both ends where it joins the base and tip. A specimen examined by Burt (1960) was tapered between the base and shaft. The baculum is well curved and possesses a small depression on the ventral side at the junction of the base and shaft. The base is dorsoventrally compressed. Measurements of the baculum are similar to those given by Burt (1960).

The ratios of the condylobasal length to the length of the distal tract and length of baculum were 4.0 and 4.6, respectively. The ratio of the length of the distal tract to the length of the baculum was 1.1.

Specimens examined.—Total (2).

Z. t. trichopus (2).—MICHOACAN: 5.3 km E Tancitaro, 1 (CM); 7 km E Tancitaro, 1 (TTU).

GEOMYS

Description

Unlike *Thomomys*, species belonging to the genus *Geomys* show very little variation in the size and shape of the phallus. The length of the distal tract ranged from 11.7 to 16.8 mm in adult individuals examined. The size relationship between the length of the distal tract and body size of individuals is much more conservative than in *Thomomys*, with ratios of the condylobasal length to the length of the distal tract ranging from 2.8 to 4.5. In all samples of *Geomys* examined the length of the distal tract was three to four times greater than the width and the short, broad glans was about half the length of the distal tract. The sides of the glans are usually recurved, terminating apically with a definite and often elaborate collar. The collar is distinct from all aspects. The pair of urethral processes vary in size and shape. Some individuals have urethral processes that may be folded and/or have serrated margins. Although the general shape of the glans appears complex compared to other geomyid rodents, features such as the midventral raphe, middorsal groove, and dorsal protuberances are usually not well-developed and often not distinct. The connection of the prepuce and glans is always distinct and often extended more apically on the dorsal side.

The epidermal structures of *Geomys* are similar to those of *Zygogeomys* in that each structure possesses multiple projections instead of a single projection as in *Thomomys* and *Orthogeomys*. The number of projections on the epidermal structures in *Geomys* is usually three but the number may vary. Epidermal structures occur between the collar and constriction and on the dorsal side of the protractile tip in all species of *Geomys*.

The baculum of all samples of *Geomys* examined consisted of a gently curving shaft which terminated in a weakly-defined tip and a weakly to strongly-defined base. The dorsal side is concave; the ventral side, although convex, often has a slight depression just anterior to the basal region. The baculum of *Geomys* shows very little variation in relative size compared to the size of the body. In adult specimens examined the length of the baculum ranged from 8.3 to 12.8 mm. The ratios of the condylobasal length to the length of the baculum and length of the distal tract to the length of the baculum ranged from 3.7 to 6.0 and 1.1 to 1.6, respectively. Like other geomyid species, the baculum is positioned between the central axis and the dorsal side of the phallus. The most discernable difference in the baculum of species of *Geomys* is variation in the shape and size of the base.

The following are detailed descriptions of the six recognized species of *Geomys*—*G. arenarius*, *G. attwateri*, *G. bursarius*, *G. personatus*, *G. pinetis*, and *G. tropicalis*. Table 4 provides measurements that apply to each description.

Geomys arenarius.—The phallus of *G. arenarius* (Fig. 14) is typical of the genus. The length of the distal tract ranged from 12.7 to 13.4 mm in five adult specimens examined. The sides of the glans tend to be strongly recurved. The collar is always expanded and distinct. Elaborate folds or convolutions along the collar are typical in *G. arenarius*. The urethral processes are well developed. Other features such as the midventral raphe, middorsal groove, and dorsal protuberances are often barely discernable. The middorsal groove is mainly evident as it passes through the collar.

Epidermal structures usually have three proximally oriented projections. However, some structures may have more projections. The shape and

Table 4.—*Standard statistics for adult specimens representing 17 samples of the five species of* Geomys.

Taxon	N	Mean	(Range) ± 2 SE	CV
		Length of distal tract		
Geomys arenarius arenarius	5	13.0	(12.7–13.4) ± 0.25	2.1
Geomys attwateri	4	13.6	(13.4–13.7) ± 0.15	1.1
Geomys bursarius jugosicularis	2	13.3	(12.7–13.9) ± 1.20	6.4
Geomys bursarius knoxjonesi	12	13.8	(12.7–15.9) ± 0.57	7.1
Geomys bursarius llanensis	2	13.3	(12.7–13.8) ± 1.10	5.8
Geomys bursarius lutescens	3	14.0	(13.7–14.2) ± 0.33	2.1
Geomys bursarius major	7	14.1	(12.5–15.8) ± 0.78	7.3
Geomys bursarius sagitallis	2	15.3	(15.0–15.5) ± 0.50	2.3
Geomys bursarius texensis	1	13.5		
Geomys personatus davisi	2	14.3	(14.0–14.7) ± 0.70	3.5
Geomys personatus maritimus	2	14.9	(14.9–14.9) ± 0.00	0.0
Geomys personatus megapotamus	7	15.8	(14.3–16.8) ± 0.63	5.3
Geomys personatus personatus	4	16.9	(15.6–19.1) ± 1.60	9.7
Geomys personatus streckeri	1	13.0		
Geomys pinetis fontanelus				
Geomys pinetis pinetis	7	12.8	(11.7–14.5) ± 0.72	7.4
Geomys tropicalis	4	13.8	(13.2–14.4) ± 0.61	4.4
		Length of glans		
Geomys arenarius arenarius	5	7.5	(6.5–8.4) ± 0.63	9.4
Geomys attwateri	4	7.1	(6.9–7.5) ± 0.25	3.5
Geomys bursarius jugosicularis	2	7.3	(6.5–8.0) ± 1.50	14.5
Geomys bursarius knoxjonesi	12	7.2	(6.7–9.0) ± 0.35	8.3
Geomys bursarius llanensis	2	6.9	(6.8–6.9) ± 0.10	1.0
Geomys bursarius lutescens	3	7.4	(7.2–7.6) ± 0.24	2.8
Geomys bursarius major	7	7.4	(6.5–8.3) ± 0.45	8.1
Geomys bursarius sagitallis	2	7.5	(7.3–7.6) ± 0.30	2.8
Geomys bursarius texensis	1	6.7		
Geomys personatus davisi	2	7.5	(7.1–7.8) ± 0.70	6.6
Geomys personatus maritimus	2	7.9	(7.9–7.9) ± 0.00	0.0
Geomys personatus megapotamus	7	8.2	(6.9–9.3) ± 0.59	9.6
Geomys personatus personatus	4	8.7	(8.5–8.9) ± 0.17	2.0
Geomys personatus streckeri	1	6.8		
Geomys pinetis fontanelus				
Geomys pinetis pinetis	7	6.3	(5.7–6.8) ± 0.28	5.9
Geomys tropicalis	4	6.6	(6.3–7.0) ± 0.30	4.5
		Length of protractile tip		
Geomys arenarius arenarius	4	2.7	(2.2–3.1) ± 0.39	14.3
Geomys attwateri	4	2.5	(1.9–2.9) ± 0.42	16.8
Geomys bursarius jugosicularis	2	3.3	(2.9–3.7) ± 0.80	17.1
Geomys bursarius knoxjonesi	12	2.6	(2.0–3.0) ± 0.16	10.9
Geomys bursarius llanensis	2	2.5	(2.4–2.6) ± 0.20	5.7
Geomys bursarius lutescens	3	3.0	(2.7–3.5) ± 0.50	14.5
Geomys bursarius major	6	2.4	(1.7–3.1) ± 0.47	23.8
Geomys bursarius sagitallis	2	2.5	(2.2–2.9) ± 0.70	19.8
Geomys bursarius texensis	1	2.4		
Geomys personatus davisi	2	3.4	(3.2–3.6) ± 0.40	8.3
Geomys personatus maritimus	2	3.3	(3.1–3.6) ± 0.50	10.7
Geomys personatus megapotamus	7	3.4	(2.7–4.2) ± 0.38	15.0
Geomys personatus personatus	3	3.1	(2.8–3.3) ± 0.29	8.1
Geomys personatus streckeri	1	2.8		
Geomys pinetis fontanelus				
Geomys pinetis pinetis	6	2.2	(1.8–2.7) ± 0.29	16.1
Geomys tropicalis	4	2.3	(2.0–2.7) ± 0.35	15.3
		Width of glans across collar		
Geomys arenarius arenarius	5	4.4	(3.5–4.8) ± 0.55	22.7
Geomys attwateri	4	3.9	(3.5–4.2) ± 0.38	9.7

Table 4.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Geomys bursarius jugosicularis	2	2.9	(2.7–3.0) ± 0.30	7.3
Geomys bursarius knoxjonesi	11	4.3	(3.9–5.1) ± 0.22	8.6
Geomys bursarius llanensis	2	3.9	(3.9–4.0) ± 0.10	1.8
Geomys bursarius lutescens	3	4.1	(3.8–4.4) ± 0.35	7.5
Geomys bursarius major	7	4.1	(3.2–4.7) ± 0.39	12.7
Geomys bursarius sagitallis	2	3.9	(3.6–4.1) ± 0.50	9.1
Geomys bursarius texensis	1	3.7		
Geomys personatus davisi	2	3.4	(3.2–3.6) ± 0.40	8.3
Geomys personatus maritimus	2	4.5	(4.5–4.5) ± 0.00	0.0
Geomys personatus megapotamus	7	4.3	(3.4–4.7) ± 0.36	11.1
Geomys personatus personatus	4	5.2	(4.7–5.8) ± 0.45	8.7
Geomys personatus streckeri	1	2.9		
Geomys pinetis fontanelus				
Geomys pinetis pinetis	7	3.5	(3.1–3.9) ± 0.22	8.2
Geomys tropicalis	4	3.9	(3.5–4.4) ± 0.40	10.4
		Width of glans across base		
Geomys arenarius arenarius	5	3.5	(3.1–4.2) ± 0.45	16.3
Geomys attwateri	4	2.9	(2.5–3.3) ± 0.34	11.6
Geomys bursarius jugosicularis	2	2.9	(2.6–3.1) ± 0.50	12.2
Geomys bursarius knoxjonesi	11	3.4	(2.9–3.8) ± 0.16	7.7
Geomys bursarius llanensis	2	3.5	(3.5–3.5) ± 0.00	0.0
Geomys bursarius lutescens	3	3.4	(3.1–4.0) ± 0.60	15.3
Geomys bursarius major	7	3.7	(3.4–4.2) ± 0.25	8.8
Geomys bursarius sagitallis	2	3.3	(3.2–3.5) ± 0.30	6.4
Geomys bursarius texensis	1	3.3		
Geomys personatus davisi	2	2.5	(2.5–2.5) ± 0.00	0.0
Geomys personatus maritimus	2	3.5	(3.1–4.0) ± 0.90	18.2
Geomys personatus megapotamus	7	3.7	(3.3–4.3) ± 0.29	10.6
Geomys personatus personatus	4	4.2	(4.0–4.4) ± 0.17	4.1
Geomys personatus streckeri	1	2.8		
Geomys pinetis fontanelus				
Geomys pinetis pinetis	7	2.8	(2.3–3.2) ± 0.28	13.5
Geomys tropicalis	4	3.1	(2.7–3.4) ± 0.31	10.0
		Length of baculum		
Geomys arenarius arenarius	5	10.8	(9.9–11.4) ± 0.54	5.6
Geomys attwateri	4	9.9	(9.3–10.7) ± 0.63	6.4
Geomys bursarius jugosicularis	2	10.5	(10.0–10.9) ± 0.90	6.1
Geomys bursarius knoxjonesi	12	11.3	(10.3–11.9) ± 0.34	5.2
Geomys bursarius llanensis	2	9.7	(9.4–9.9) ± 0.50	3.6
Geomys bursarius lutescens	3	10.9	(9.8–12.1) ± 1.34	10.6
Geomys bursarius major	7	10.9	(10.4–11.5) ± 0.30	3.6
Geomys bursarius sagitallis	2	11.0	(10.8–11.2) ± 0.40	2.6
Geomys bursarius texensis	1	9.2		
Geomys personatus davisi	2	11.3	(11.1–11.5) ± 0.40	2.5
Geomys personatus maritimus	2	11.5	(10.5–12.6) ± 2.09	12.9
Geomys personatus megapotamus	7	11.6	(10.6–12.1) ± 0.46	5.2
Geomys personatus personatus	4	12.1	(11.2–12.8) ± 0.73	6.0
Geomys personatus streckeri	1	9.6		
Geomys pinetis fontanelus	1	9.9		
Geomys pinetis pinetis	7	9.3	(8.3–10.5) ± 0.62	8.8
Geomys tropicalis	4	9.9	(9.3–10.4) ± 0.50	5.0
		Width of bacular base		
Geomys arenarius arenarius	5	1.6	(1.2–1.8) ± 0.21	14.9
Geomys attwateri	4	2.1	(1.8–2.4) ± 0.26	12.6
Geomys bursarius jugosicularis	2	2.3	(2.2–2.3) ± 0.10	3.1
Geomys bursarius knoxjonesi	12	1.9	(1.6–2.4) ± 0.15	14.1
Geomys bursarius llanensis	2	1.9	(1.8–2.0) ± 0.20	7.4

Table 4.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Geomys bursarius lutescens	3	2.1	(1.8–2.3) ± 0.55	12.6
Geomys bursarius major	7	2.1	(1.5–2.8) ± 0.35	21.8
Geomys bursarius sagitallis	2	2.2	(2.1–2.3) ± 0.20	6.4
Geomys bursarius texensis	1	2.2		
Geomys personatus davisi	2	1.7	(1.5–1.8) ± 0.30	12.5
Geomys personatus maritimus	2	2.1	(1.8–2.3) ± 0.50	16.8
Geomys personatus megapotamus	7	1.9	(1.6–2.0) ± 0.14	10.0
Geomys personatus personatus	4	2.1	(1.9–2.3) ± 0.17	8.2
Geomys personatus streckeri	1	1.6		
Geomys pinetis fontanelus	1	2.4		
Geomys pinetis pinetis	7	2.3	(1.9–2.7) ± 0.22	12.7
Geomys tropicalis	4	1.6	(1.3–1.9) ± 0.27	17.2
		Height of bacular base		
Geomys arenarius arenarius	5	1.6	(1.1–1.8) ± 0.27	19.0
Geomys attwateri	4	1.8	(1.7–2.0) ± 0.15	8.3
Geomys bursarius jugosicularis	2	1.5	(1.5–1.6) ± 0.10	4.7
Geomys bursarius knoxjonesi	12	1.9	(1.5–2.3) ± 0.15	13.7
Geomys bursarius llanensis	2	1.2	(1.1–1.3) ± 0.20	11.8
Geomys bursarius lutescens	3	1.6	(1.4–1.8) ± 0.23	12.5
Geomys bursarius major	7	1.6	(1.4–2.0) ± 0.16	12.9
Geomys bursarius sagitallis	2	1.9	(1.7–2.0) ± 0.30	11.2
Geomys bursarius texensis	1	1.6		
Geomys personatus davisi	2	1.7	(1.7–1.8) ± 0.05	4.1
Geomys personatus maritimus	2	2.0	(1.7–2.3) ± 0.60	21.2
Geomys personatus megapotamus	7	1.8	(1.5–2.1) ± 0.17	12.4
Geomys personatus personatus	4	2.0	(1.7–2.2) ± 0.22	10.8
Geomys personatus streckeri	1	1.3		
Geomys pinetis fontanelus	1	1.9		
Geomys pinetis pinetis	7	1.3	(1.2–1.5) ± 0.09	8.7
Geomys tropicalis	4	1.5	(1.3–1.8) ± 0.22	14.8
		Condylobasal length		
Geomys arenarius arenarius	5	46.0	(45.4–47.0) ± 0.55	1.3
Geomys attwateri	4	43.2	(41.2–44.4) ± 1.49	3.5
Geomys bursarius jugosicularis	2	44.6	(43.4–45.8) ± 2.41	3.8
Geomys bursarius knoxjonesi	12	43.9	(40.5–45.2) ± 0.79	3.1
Geomys bursarius llanensis	2	42.2	(41.2–43.2) ± 2.01	3.3
Geomys bursarius lutescens	3	48.1	(44.3–51.1) ± 4.00	7.2
Geomys bursarius major	7	47.0	(44.2–50.1) ± 1.86	5.2
Geomys bursarius sagitallis	2	44.7	(44.2–45.2) ± 1.00	1.6
Geomys bursarius texensis	1	40.5		
Geomys personatus davisi	2	47.6	(44.8–50.5) ± 5.68	8.5
Geomys personatus maritimus	2	52.9	(51.8–54.1) ± 2.31	3.1
Geomys personatus megapotamus	7	50.4	(47.0–52.5) ± 1.52	4.0
Geomys personatus personatus	4	56.7	(55.7–57.8) ± 0.93	1.6
Geomys personatus streckeri	1	38.5		
Geomys pinetis fontanelus	1	43.7		
Geomys pinetis pinetis	7	50.3	(46.7–52.4) ± 1.65	4.3
Geomys tropicalis	4	46.6	(44.1–49.4) ± 2.18	4.7
		Length of hind foot		
Geomys arenarius arenarius	5	33.2	(32–35) ± 0.98	3.3
Geomys attwateri				
Geomys bursarius jugosicularis	2	32.5	(32–33) ± 1.00	2.2
Geomys bursarius knoxjonesi	9	32.2	(30–35) ± 1.19	5.5
Geomys bursarius llanensis				
Geomys bursarius lutescens	3	33.3	(30–35) ± 3.34	8.7
Geomys bursarius major	3	33.7	(31–35) ± 2.67	6.9
Geomys bursarius sagitallis	1	30		

Table 4.—*Continued.*

Taxon	N	Mean	(Range) ± 2 SE	CV
Geomys bursarius texensis				
Geomys personatus davisi	2	36.5	(35–37) ± 3.01	5.8
Geomys personatus maritimus	1	37		
Geomys personatus megapotamus	4	36.7	(36–39) ± 1.50	2.7
Geomys personatus personatus	4	39.7	(39–42) ± 1.71	4.3
Geomys personatus streckeri				
Geomys pinetis fontanelus	1	33		
Geomys pinetis pinetis	7	33.7	(32–37) ± 1.36	5.3
Geomys tropicalis	4	31.5	(30–33) ± 12.9	4.1

pattern of the structures is relatively uniform, but the size may be variable.

The baculum (Fig. 14) is typical of the genus with a distinct base, shaft, and tip. The length of the baculum ranged from 9.9 to 11.4 mm among five adult specimens examined. The baculum is slightly curved. The base is bulbous with the sides, viewed dorsoventrally, gradually tapering to the shaft. The width of the base may be larger, smaller, or equal to the height of the base.

For five specimens of *G. arenarius* the mean ratios (range in parentheses) of the condylobasal length to the length of the distal tract and length of baculum were 3.5 (3.4–3.6) and 4.2 (4.0–4.6), respectively; the length of the distal tract to the length of the baculum was 1.2 (1.1–1.3).

Specimens examined.—Total (7).

G. a. arenarius (7).—NEW MEXICO: *Dona Ana Co.:* W Las Cruces on Rio Grande, 1 (TTU). TEXAS: *El Paso Co.:* 2.5 mi N Rio Grande, 30 mi E El Paso, 1 (TTU); 1 mi S Fabens, 5 (TTU).

Geomys attwateri.—The phallus of *G. attwateri* (Fig. 15) is similar to that of *G. arenarius* except

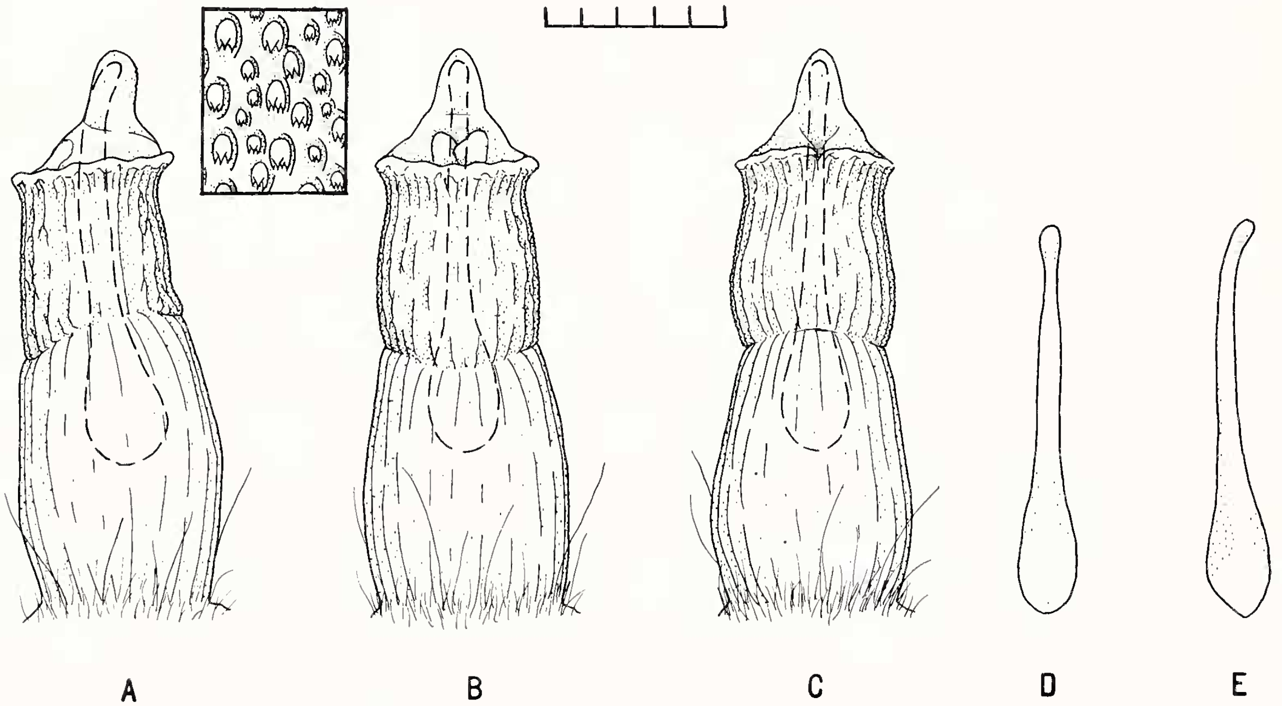

Fig. 14.—Phallus and baculum of *Geomys arenarius arenarius* from Texas: El Paso Co., 1 mi S Fabens (TTU 17554), illustrated as in Fig. 1.

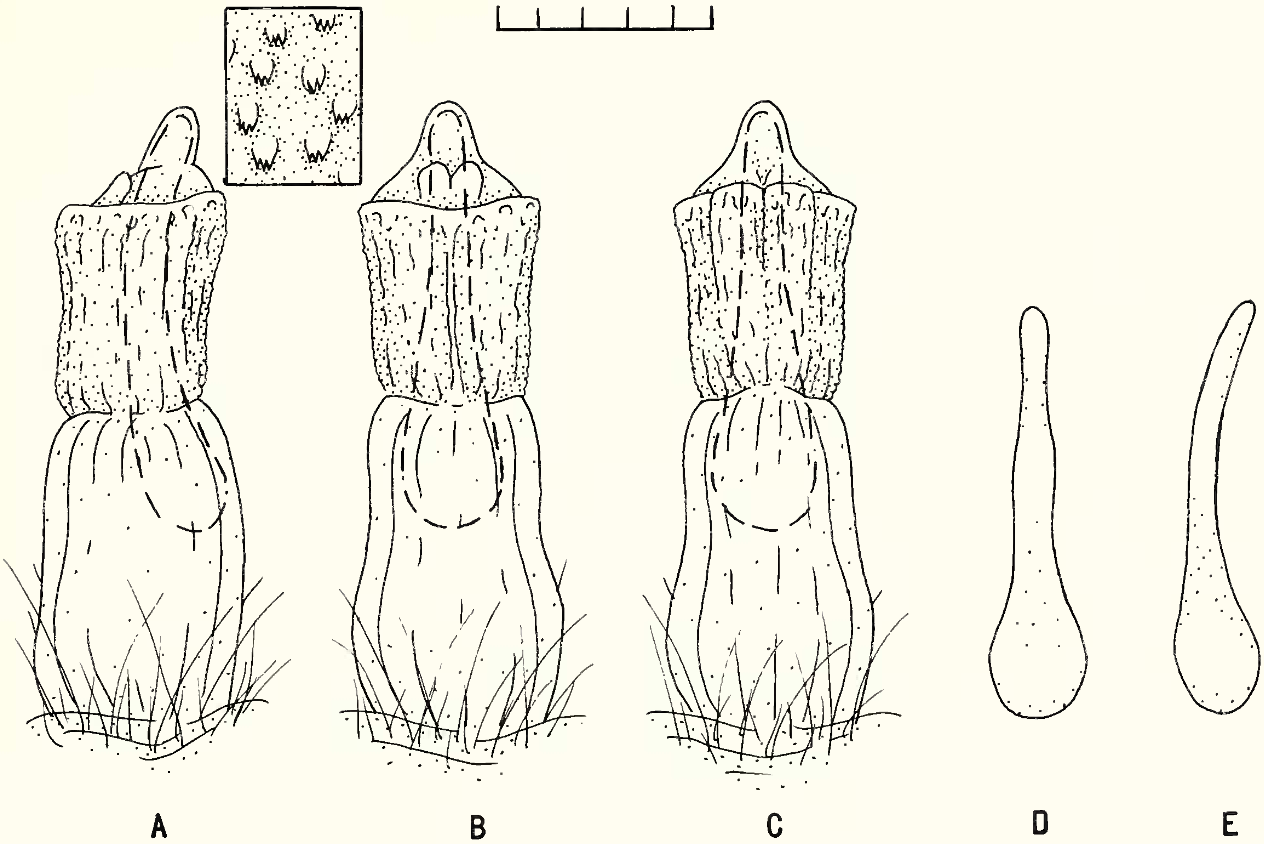

Fig. 15.—Phallus and baculum of *Geomys attwateri* from Texas: Milam Co., 0.8 mi N, 1.3 mi E Milano (TTU 19137), illustrated as in Fig. 1.

that it tends to be slightly larger. The length of the distal tract ranged from 13.4 to 13.7 mm in four adult specimens examined. The collar, constriction, urethral processes, midventral raphae, and epidermal structures resemble that of *G. arenarius.* However, *G. attwateri* tends to have a middorsal groove and dorsal protuberances that are more distinct.

The baculum of *G. attwateri* (Fig. 15) has features, shape, and size similar to that of *G. arenarius.* The length of the baculum of four adult specimens examined ranged from 9.3 to 10.7 mm. The base tends to be dorsoventrally compressed. The description and length of the bacula examined correspond to those given by Kennerly (1958), except that the average width of the base was greater in the series of adults examined in this study.

The mean ratio (range in parentheses) of the condylobasal length to the length of the distal tract for four adult *G. attwateri* was 3.2 (3.1–3.3); condylobasal length to the length of the baculum was 4.4 (4.0–4.8); length of the distal tract to the length of the baculum was 1.4 (1.3–1.5).

Specimens examined.—Total (10).

G. attwateri (10).—TEXAS: *Gonzales Co.:* 2.2 mi N Nixon, 1 (TTU); *Milam Co.:* 1.3 mi N, 3 mi E Milano, 1 (TTU); 1.1 mi N, 2.5 mi E Milano, 3 (TTU); 0.8 mi N, 1.3 mi E Milano, 2 (TTU); 1.3 mi S, 3.3 mi W Milano, 1 (TTU); *San Patricio Co.:* between Aransas Pass and Ingleside on Hwy. 361, 2 (TTU).

Geomys bursarius.—The phallus of *G. bursarius* (Fig. 16) is similar to that of *G. attwateri.* The length of the distal tract ranged from 12.5 to 15.9 mm in adult specimens examined. Basic features, such as the collar, constriction, urethral processes, midventral raphe, and epidermal structures are similar to those of *G. attwateri.*

The baculum of *G. bursarius* (Fig. 16) is very similar to *G. arenarius* in size and shape. Bacular length ranged from 9.2 to 11.9 mm in adult specimens examined. The base of the baculum of *G. bursarius* is almost always dorsoventrally compressed. The tip is distinct and slightly expanded laterally. Description and dimensions of bacula of *G. bursarius* examined in this study closely correspond to findings of Burt (1960).

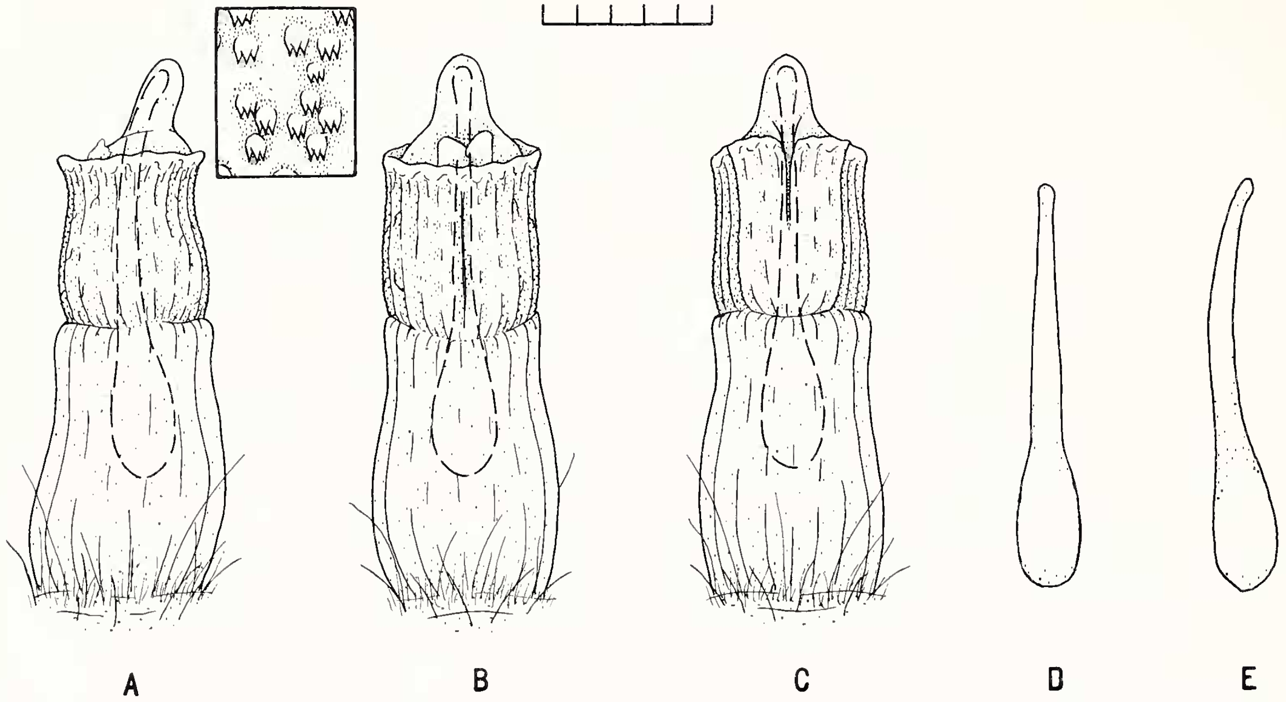

Fig. 16.—Phallus and baculum of *Geomys bursarius knoxjonesi* from Texas: Gaines Co., 0.8 mi S, 15 mi E Seminole (TTU 19157), illustrated as in Fig. 1.

In adult specimens of subspecies of *G. bursarius* examined, the ratio of the condylobasal length to the length of the distal tract ranged from 2.8 to 3.7; condylobasal length to the length of the baculum ranged from 3.7 to 4.8; length of the distal tract to the length of the baculum ranged from 1.1 to 1.5.

Specimens examined.—Total (60).

G. b. industrius (1).—KANSAS: *Ford Co.:* 13 mi S Dodge City, 1 (KU).

G. b. jugossicularis (2).—COLORADO: *Prowers Co.:* Lamar, 3,663 ft, 2 (TTU).

G. b. knoxjonesi (26).—TEXAS: *Cochran Co.:* 0.5 mi N, 1.8 mi W Morton, 1 (TTU); 4 mi S, 0.2 mi E Morton, 1 (TTU); 2.5 mi N, 2.5 mi W Whiteface, 1 (TTU); *Gaines Co.:* 5 mi SW Seagraves on Hwy. 385, 2 (TTU); 3 mi N Seminole, 1 (TTU); 0.8 mi S, 15 mi E Seminole, 5 (TTU); *Winkler Co.:* 10 mi NE Kermit on Hwy. 115, 3 (TTU); 4.1 mi N, 5.1 mi E Kermit, 10 (TTU); 0.3 mi N, 2.5 mi E Kermit, 2 (TTU).

G. b. llanensis (5).—TEXAS: *Llano Co.:* 2.6 mi N, 1.8 mi E Castell, 2 (TTU); 9.2 mi S, 11 mi E Kingsland, 1 (TTU); 10 mi S, 1.8 mi E Kingsland, 1 (TTU); 0.2 mi N, 8.7 mi W Llano, 1 (TTU).

G. b. lutescens (3).—KANSAS: *Ellis Co.:* 3 mi S Antonio, 1 (TTU). NEBRASKA: *Garden Co.:* 30 mi N, 2.0 mi W Oshkosh, 3,850 ft, 2 (CM).

G. b. major (12).—NEW MEXICO: *Guadalupe Co.:* 1 mi SW Santa Rosa, 1 (TTU). TEXAS: *Collingsworth Co.:* 2 mi N, 9 mi W Wellington, 4 (TTU); *McLennon Co.:* 1 mi S Waco, 3 (TTU); *Mitchell Co.:* 3 mi N, 0.3 mi E Colorado City, 4 (TTU).

G. b. missouriensis (2).—MISSOURI: *St. Louis Co.:* 3.2 mi N, 2.3 mi E Manchester, 1 (TTU); 1.9 mi N, 0.3 mi E Manchester, 1 (TTU).

G. b. sagittalis (3).—TEXAS: *Galveston Co.:* 2 mi N Texas City, 1 (TTU); *Montague Co.:* 3.1 mi E Jct. 59 and Fm. Rd. 1758 on Fm. Rd. 1758, 1 (TTU); *Robertson Co.:* 3.4 mi N, 2 mi W Calvert, 1 (TTU).

G. b. texensis (6).—TEXAS: *Mason Co.:* 0.3 mi S, 1.5 mi W Castell, 3 (TTU); 0.3 mi S, 0.8 mi W Castell, 1 (TTU); 0.7 mi S, 2.1 mi W Castell, 1 (TTU); 1 mi N, 1.1 mi W Mason, 1 (TTU).

Geomys personatus.—The phallus of *G. personatus* (Fig. 17) is basically shaped like that of other members of the genus. Subspecies of *G. personatus* include some of the largest (*G. p. personatus*) and smallest (*G. p. streckeri*) members of the genus *Geomys*. Proportionally the size of the phallus follows this pattern. The length of the distal tract is three to four times the width, and the length of the glans is about half the length of the distal tract. The length of the distal tract in *G. personatus* ranged from 13.0 to 19.1 mm in adult specimens examined. The sides of the glans, viewed dorsoventrally, are straight or slightly recurved and gradually expand

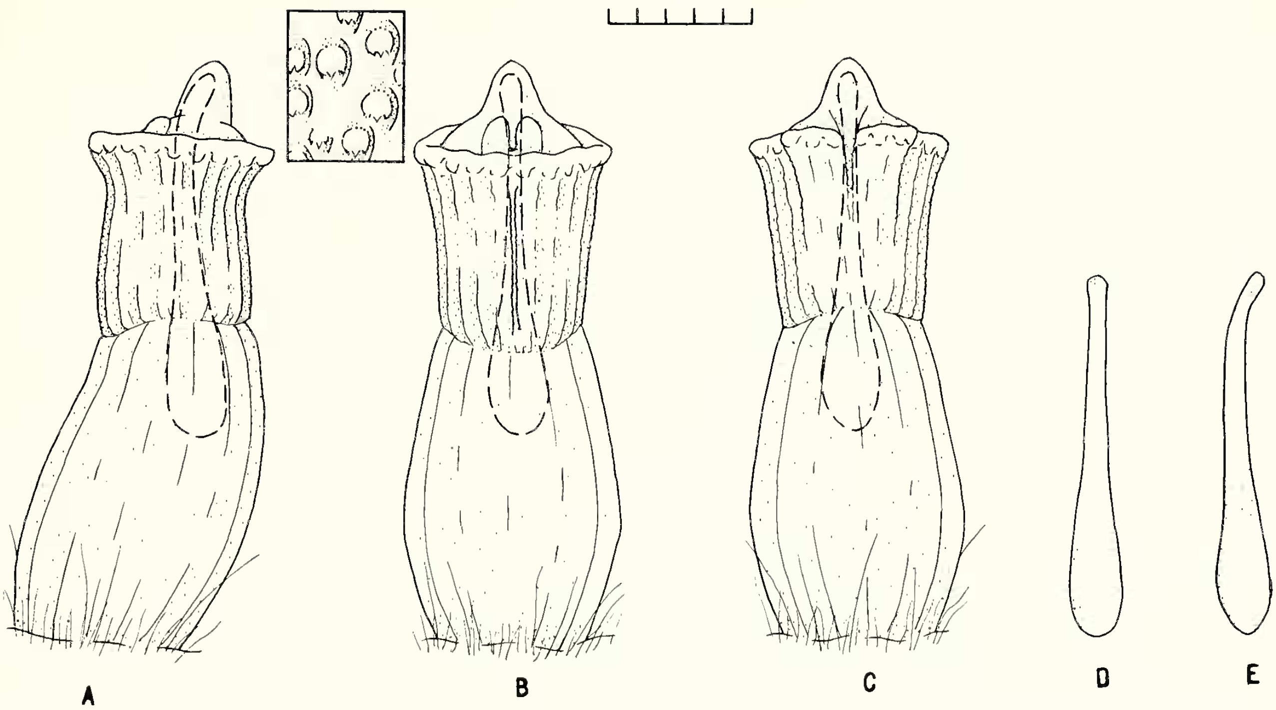

Fig. 17.—Phallus and baculum of *Geomys personatus personatus* from Texas: Nueces Co., Mustang Island, Access Road No. 2 (TTU 15356), illustrated as in Fig. 1.

apically to the collar. The presence and distinctness of the collar, constriction, urethral processes, midventral raphe, middorsal groove, dorsal protuberances, and epidermal structures are basically the same as *G. bursarius* with the primary distinction being proportionally different sizes.

The baculum of *G. personatus* (Fig. 17) is basically the same shape as *G. arenarius*, *G. attwateri*, and *G. bursarius*. The size of the baculum varies proportionally among subspecies of *G. personatus* with the length ranging from 9.6 to 12.8 mm among adult specimens examined. The range of these measurements is in agreement with material examined by Kennerly (1958). Although there is a tendency for the base of the baculum to be dorsoventrally compressed, this trend is not always true because the width of the base may occasionally be less than or equal to the height.

Among the subspecies of *G. personatus* examined the ratios of the condylobasal length to the length of the distal tract and to the length of the baculum ranged from 2.9 to 3.7 and 4.0 to 5.0, respectively. The ratio of the length of the distal tract to the length of the baculum ranged from 1.2 to 1.6.

Specimens examined.—Total (29).

G. p. davisi (2).—TEXAS: *Zapata Co.:* 3 mi N, 2.8 mi W Zapata, 2 (CM).

G. p. fallax (1).—TEXAS: *Bee Co.:* 0.8 mi N, 4.3 mi W Beeville, 1 (TTU).

G. p. maritimus (3).—TEXAS: *Nueces Co.:* Flour Bluff, 8.0 mi S, 8.3 mi E Corpus Christi, 3 (TTU).

G. p. megapotamus (13).—TAMAULIPAS: barrier island, approx. 70 mi S Rio Grande, 1 (TTU); barrier island, 10 mi N Boca Santa Maria, 6 (TTU); barrier island, 5 mi S road at Washington Beach, 1 (TTU). TEXAS: *Duval Co.:* 3 mi S, 24.6 mi E Hebbronville, 5 (TTU).

G. p. personatus (8).—TEXAS: *Nueces Co.:* Mustang Island, Access Rd. No. 2, 7 (TTU); Mustang Island, 7 mi S, 4 mi W Port Aransas, 1 (TTU).

G. p. streckeri (2).—TEXAS: *Dimmit Co.:* near Carrizo Springs, 2 (TTU).

Geomys pinetis.—The phallus of *G. pinetis* (Fig. 18) maintains the general shape and relative size of *G. arenarius*, *G. attwateri*, and *G. bursarius*. The length of the distal tract, ranged from 11.7 to 14.5 mm in seven adult specimens examined. The length of the glans tends to be less than half the length of the distal tract. The shape of the glans has minor differences from that of other *Geomys*. The sides of the glans, viewed dorsoventrally, are more or

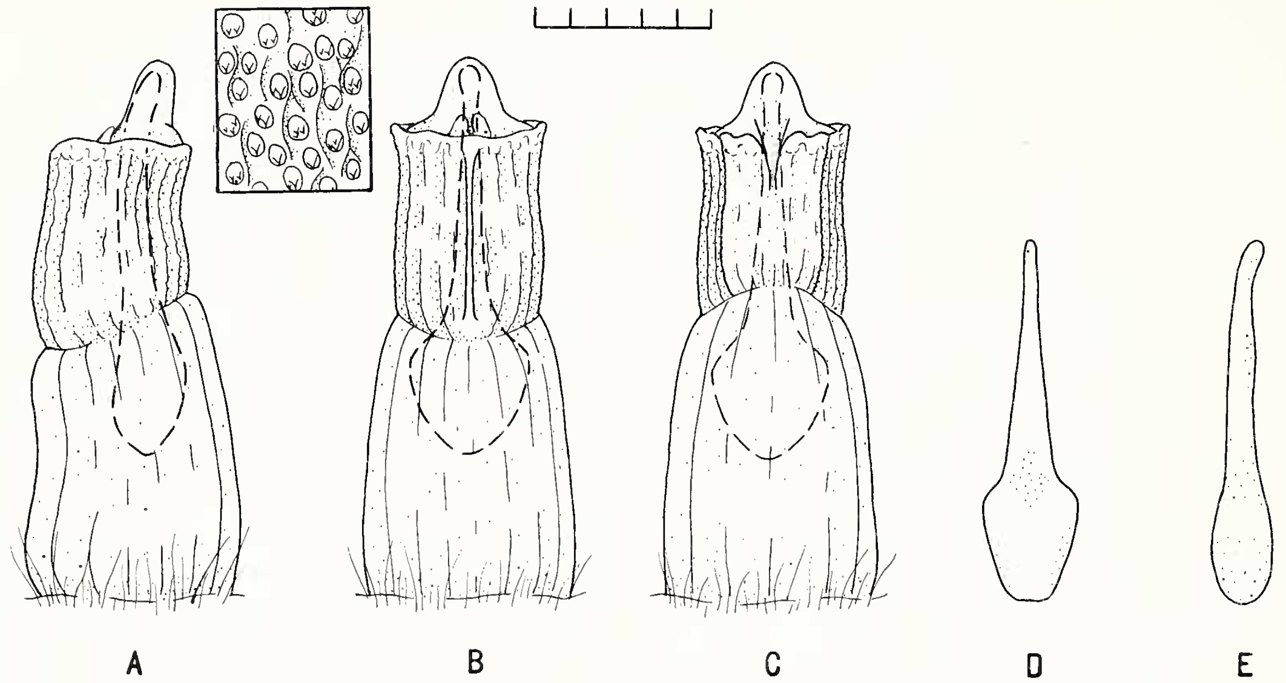

Fig. 18.—Phallus and baculum of *Geomys pinetis pinetis* from Florida: Duval Co., 1.0 mi NW Bayard on Hwy. 1 (TTU 16619), illustrated as in Fig. 1.

less straight and parallel with a slight flare at the collar. Viewed laterally, the ventral side may be somewhat convex or straight and the dorsal side recurved. Although the collar is less flared than other *Geomys*, it is still a distinct feature, as is the constriction which is often strongly extended apically on the dorsal side. In *G. pinetis* the urethral processes often appear reduced. The midventral raphe is well developed. The development of the middorsal groove and dorsal protuberances is similar to that of *G. attwateri*, *G. bursarius*, and *G. personatus*. The size and pattern of epidermal structures is relatively uniform and is similar to that of other members of the genus.

The baculum of *G. pinetis* (Fig. 18) ranged in length from 8.3 to 10.5 mm in seven adult specimens examined. The width of the base is always greater than the height of the base. One of the most striking characteristics found in *G. pinetis*, that sets it apart from other *Geomys*, is the shape of the base of the baculum. Viewed dorsoventrally, the base of the baculum has sides that expand apically and then converge sharply to join the shaft, instead of gradually tapering to the shaft as in other members of the genus. This study found this character to be consistent in all specimens examined, including the holotype and a paratype of *G. p. fontanelus*. Sherman (1940) reported no differences between the baculum of *G. p. fontanelus* and other populations of *G. pinetis*.

In seven adult specimens of *G. p. pinetis* the mean ratios (range in parentheses) of the condylobasal length to the length of the distal tract and length of the baculum were 3.9 (3.5–4.5) and 5.4 (4.9–6.0), respectively. The ratio of the length of the distal tract to the length of the baculum averaged 1.4 and ranged from 1.2 to 1.6.

Specimens examined.—Total (19).

G. p. fontanelus (2).—Georgia: *Chatham Co.:* 8 mi NW Savannah, 2 (FSM).

G. p. pinetis (17).—Florida: *Alachua Co.:* 1 mi N, 2.8 mi W Alachua, 1 (CM); 0.5 mi S, 2 mi E Alachua, 1 (CM); 1.4 mi NW Jct. Hwy. 24 and Hwy. 41, 1 (TTU); 0.9 mi SW Jct. I-75 and Hwy. 24, 1 (TTU); 3.4 mi SW Jct. I-75 and Hwy. 24, 1 (TTU); 3.4 mi SW Jct. I-75 and Hwy. 24, 1 (TTU); *Calhoun Co.:* 1.2 mi N Clarksville, 1 (TTU); *Duval Co.:* 1.0 mi NW Bayard on Hwy. 1, 1 (TTU); *Highlands Co.:* Sebring, 2 (CM); *Hillsborough Co.:* Tampa, vicinity University of South Florida, 5 (TTU); *Walton Co.:* 1.1 mi E county line on Hwy. 90, 1 (TTU). Georgia: *Camden Co.:* 1.1 mi NE Kingsland, 1 (TTU).

Geomys tropicalis.—The phallus of *G. tropicalis* (Fig. 19) resembles *G. personatus* except for size

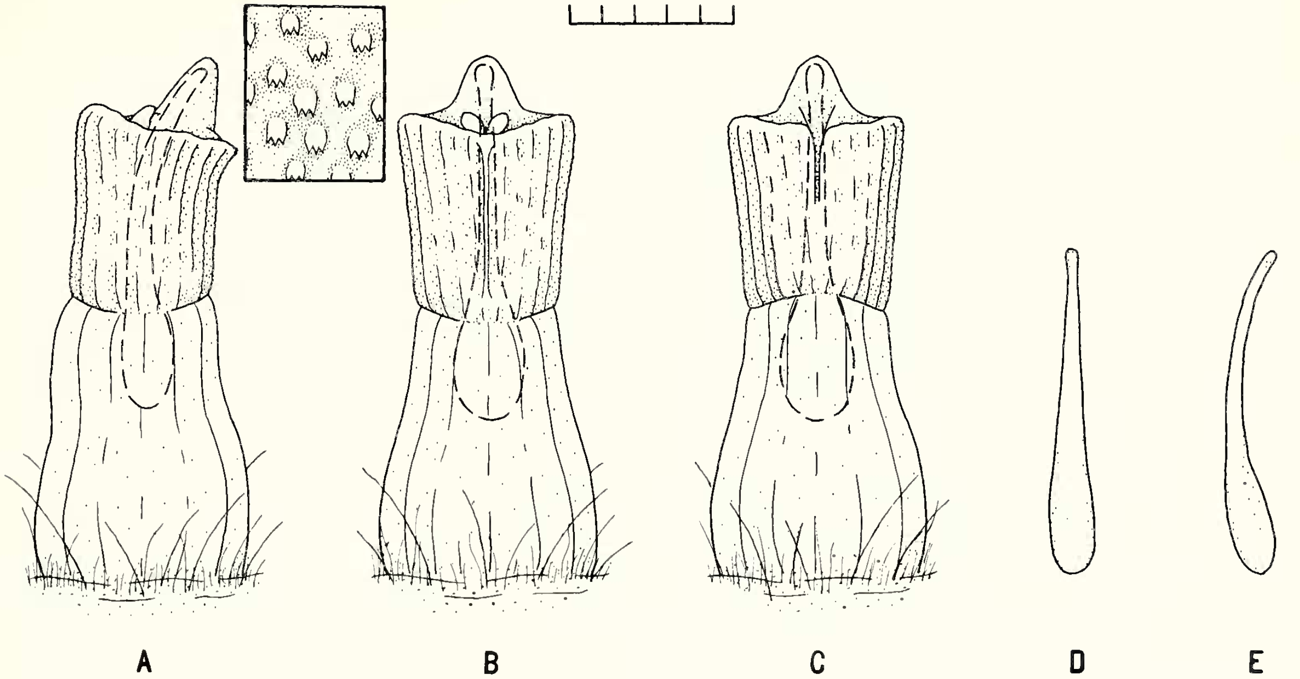

Fig. 19.—Phallus and baculum of *Geomys tropicalis* from Tamaulipas: 2.5 mi SE Altamira (TTU 14318), illustrated as in Fig. 1.

variation. The length of the distal tract ranged from 13.2 to 14.4 mm in four adult specimens examined. Like *G. personatus*, the sides of the glans of *G. tropicalis*, viewed dorsoventrally, are more or less straight and are parallel or expanded apically to the collar. The collar is distinct but may not share the elaborate convolutions found in other species of *Geomys*. The development of the midventral raphe, middorsal groove, dorsal protuberances, and epidermal structures resembles that of *G. personatus*.

The baculum of *G. tropicalis* (Fig. 19) is basically the same as the other species of *Geomys*, except *G. pinetis*. The length of the baculum of four adult specimens examined ranged from 9.3 to 10.4 mm. In all four specimens the width of the base almost equalled the height of the base.

The mean ratio (range in parentheses) of the condylobasal length to the length of the distal tract for four adult *G. tropicalis* was 3.4 (3.1–3.5); condylobasal length to the length of the baculum was 4.7 (4.5–5.0); length of the distal tract to the length of the baculum was 1.4 (1.3–1.5).

Specimens examined.—Total (10).

G. tropicalis (10).—TAMAULIPAS: 2.5 mi SE Altamira, 9 (TTU); 2.5 mi SSE Altamira, 1 (TTU).

Statistics

Age variation in *Geomys* was observed in this study and reported by Kennerly (1958). However, the amount of age variation was not analyzed in the present study. Table 4 provides the standard statistics (sample size, mean, range, standard error, and coefficient of variation) for adult specimens of *Geomys* examined.

Examination of individual variation was conducted on a representative sample from different species of *Geomys*. Each sample used included individuals taken from a restricted geographical area that would be assumed to be part of a continuous population. The taxa examined for individual variation were *G. arenarius arenarius*, *G. attwateri*, *G. personatus personatus*, *G. pinetis pinetis*, and *G. tropicalis*. Coefficients of variation for phallic and bacular measurements ranged from 1.1 to 22.7. The average coefficients of variation for the above taxa were 13.0, 8.7, 7.2. 10.2, and 10.2, respectively. The characters that generally had the lowest values for coefficients of variation were the length of the distal tract, length of the glans, and length of the baculum. The highest values were found among different characters for different species. However, the length of the protractile tip consistently had high values, as indicated by a mean coefficient of variation of 14.1 for the five samples examined. The characters having the lowest and highest coefficients of variation in *G. arenarius* were length of distal tract (2.1) and width of glans across collar (22.7); in *G. attwateri,* length of distal tract (1.1) and width of bacular base (12.6); in *G. personatus,* length of glans (2.0) and height of bacular base (10.8); in *G. pinetis,* length of glans (5.9) and length of protractile tip (16.1); in *G. tropicalis,* length of distal tract (4.4) and width of bacular base (17.2).

Because several nominal subspecies of *G. bursarius* were available for this study, an attempt was made to determine if geographical variation of phallic and bacular characters does occur in *Geomys.* The limited geographical coverage of samples precluded quantifying the amount of geographical variation that might exist. Examination of ranked means of samples of *G. bursarius* generally revealed no consistencies in size for all of the characters. Taxa ranked among the largest for one or more characters may rank among the smallest in other characters. However, taxa from south-central Texas (*G. b. llanensis* and *G. b. texensis*) tended to group together and have smaller-sized individuals. The only other trend observed among ranked means of *G. bursarius* was that *G. b. lutescens* and *G. b. major* were grouped together in six of eight characters. Based on these observations it is assumed that better geographical coverage of samples, and larger sample sizes may reveal greater geographical variation than was found in these samples of *G. bursarius.* However, it is unlikely the amount of variation would approach that observed in members of the genus *Thomomys.*

Examination of variation among species of *Geomys* was conducted, using samples with at least three individuals. Subspecies within a species were not combined to form a single group because of possible problems of geographical variation and biased representation. The samples used were *G. arenarius, G. attwateri, G. bursarius knoxjonesi, G. b. lutescens, G. b. major, G. personatus megapotamus, G. p. personatus, G. pinetis,* and *G. tropicalis.* Univariate and SS-STP analyses of these samples were performed with the UNIVAR (Power, 1970) computer program. Analysis of variance revealed significant differences ($P \leq 0.05$) for all phallic and bacular characters. *G. p. personatus* had the highest mean for all phallic and bacular characters except for the length of the protractile tip and width of the bacular base, where it ranked second; *G. p. megapotamus* had the highest mean for the length of the protractile tip and was ranked second, third, and fourth in highest means for three, two, and one characters, respectively. The lowest mean for all characters, except the width of bacular base, was found in *G. pinetis*; *G. pinetis* had the highest mean for width of the baculum thus supporting this character as being diagnostic for the species (see description). *G. tropicalis* was ranked among the smallest in the samples examined with rankings of first, second, and third smallest in one, five, and one characters, respectively. *G. attwateri* also ranked among the smallest with five of seven characters ranking either second or third smallest of the samples examined. *G. arenarius* and *G. bursarius* showed no specific trends in relationships of means. The SS-STP analysis provided broadly overlapping nonsignificant subsets for all phallic and bacular characters. Only the length of distal tract and length of glans had cases of nonoverlapping subsets. In the three subsets formed with the length of the distal tract the two nonoverlapping subsets were formed with the two samples of *G. personatus* in one subset and the remaining samples in the other subset. An intermediate subset consisting of *G. p. megapotamus, G. b. major,* and *G. b. lutescens* overlapped slightly with the other two subsets. For the length of the glans four nonsignificant subsets were formed. A subset consisting of *G. p. personatus, G. p. megapotamus,* and *G. arenarius* did not overlap with the subset of the smaller-sized (in ranked order) *G. b. lutescens, G. b. knoxjonesi, G. attwateri, G. tropicalis,* and *G. pinetis.* Two intermediate subsets broadly overlapped with each other and the two subsets previously discussed. In the remaining characters two subsets were formed with the length of protractile tip; three subsets were formed with width of glans across collar, and the bacular characters; four subsets were formed with the width of glans across base.

Variation between species of *Geomys* was examined by multivariate analysis, using sample means with the MINT statistical computer program. The samples of *Geomys* used in the multivariate analysis, followed by the corresponding reference number, were *G. arenarius* (1), *G. attwateri* (2), seven subspecies of *G. bursarius* (*jugossicularis,* 3; *knoxjonesi,* 4; *llanensis,* 5; *lutescens,* 6; *major,* 7; *sagittalis,* 8; *texensis,* 9), five subspecies of *G.*

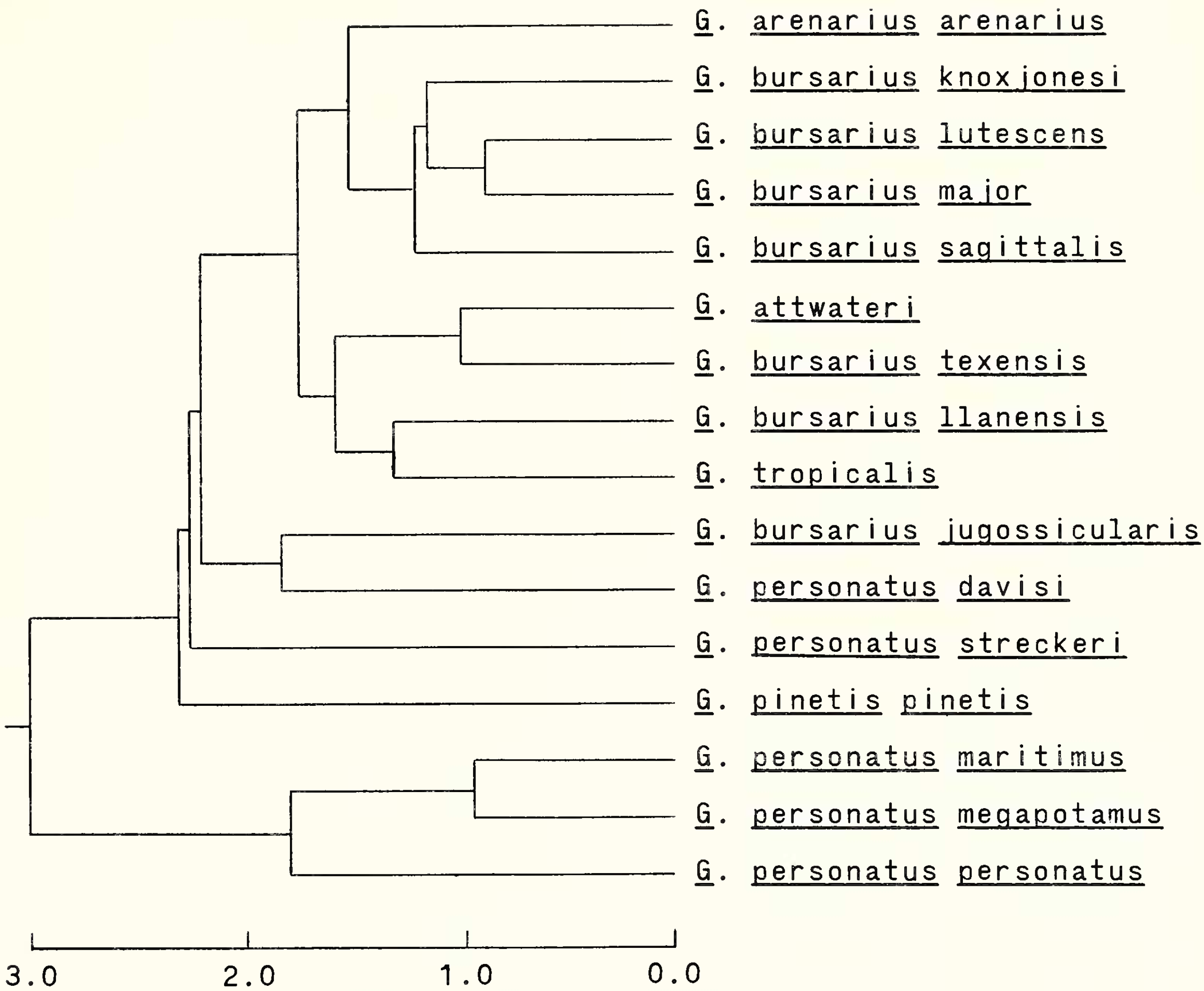

Fig. 20.—Distance phenogram of 16 samples of *Geomys* resulting from clustering by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.727.

personatus (*davisi*, 10; *maritimus*, 11; *megapotamus*, 12; *personatus*, 13; *streckeri*, 14), *G. pinetis* (15), and *G. tropicalis* (16).

The distance phenogram produced by the MINT program is illustrated in Fig. 20. The cophenetic correlation value for this phenogram is 0.727. The phenogram forms two groups. One group consists of the larger members of *G. personatus*—*personatus*, *megapotamus*, and *maritimus*. The second group subdivides into a group represented by *G. pinetis* and series of additional clusters including samples of the other taxa of *Geomys*. In the next subdivision *G. p. streckeri* is distinctly separated and followed by a group consisting of *G. p. davisi* and *G. b. jugossicularis* which remain relatively distinct from each other. The remaining subspecies of *G. bursarius* form two clusters. The first cluster includes *G. b. knoxjonesi*, *G. b. lutescens*, *G. b. major*, and *G. b. sagittalis*. The second cluster includes *G. b. texensis* and *G. b. llanensis*. *Geomys arenarius* was placed with the first cluster of *G. bursarius*; *G. attwateri* and *G. tropicalis* were placed with the second cluster.

The first three principal components extracted from the matrix of correlation among characters is illustrated in Fig. 21. Four of the five samples of *G. personatus* (10, 11, 12, 13) form a loose grouping toward the right side of the plot. Samples of *G.*

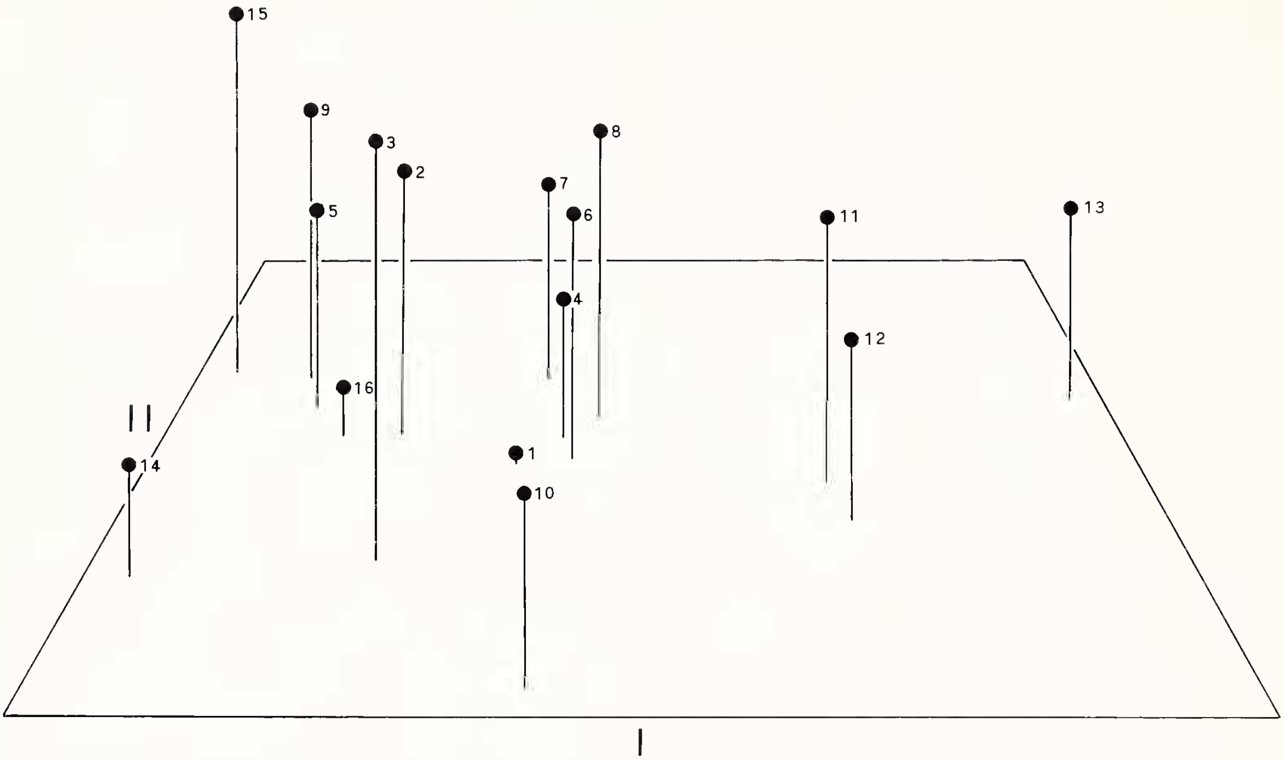

Fig. 21.—Three-dimensional projection of 16 samples of *Geomys* (*G. arenarius*, 1; *G. attwateri*, 2; *G. bursarius*, 3–9; *G. personatus*, 10–14; *G. pinetis*, 15; *G. tropicalis*, 16) onto the first three principal components based upon a matrix of correlation among one cranial, five phallic, and three bacular measurements. Components I and II are indicated in the plots and component III is represented by height.

bursarius, (3, 4, 5, 6, 7, 8, 9) and *G. attwateri* (2) also form a loose, but unified group in the upper left side of the plot. The remaining taxa—*G. arenarius* (1), *G. pinetis* (15), *G. tropicalis* (16), and *G. p. streckeri* (14)—are situated toward the left side of the plot. *G. pinetis* (15) and *G. p. streckeri* (14) are separated from all other taxa in component I, and separated from each other in component II. *G. pinetis* plots closer to *G. bursarius* than any other taxa. *G. arenarius* (1), *G. p. streckeri* (14), and *G. tropicalis* (16) are separated from each other with all three components and separated from the remaining taxa in component III.

Table 5.—*Factor matrix from correlation among nine characters of the five species (16 samples) of* Geomys *examined.*

Character	Component I	Component II	Component III
Condylobasal length	0.785	−0.085	0.155
Length of distal tract	0.908	−0.012	0.065
Length of glans	0.950	0.196	−0.010
Length of protractile tip	0.565	0.743	0.193
Width of glans across collar	0.807	−0.439	−0.322
Width of glans across base	0.723	−0.499	−0.269
Length of baculum	0.918	0.262	−0.046
Width of bacular base	0.135	−0.451	0.870
Height of bacular base	0.817	0.009	0.121

The amount of phenetic variation explained by components I, II, and III are 59.6%, 14.6%, and 11.3%, respectively. Results of principal component analyses showing the influence of each character for the first three components are given in Table 5. All characters except the width of the baculum are heavily weighted in the first factor. The length of the distal tract, length of the glans, and length of the baculum had the highest values in component I. In components II and III the characters with heavy weightings were the length of the protractile tip and width of bacular base, respectively.

Pappogeomys

Description

Pappogeomys bulleri.—In this study the genus *Pappogeomys* is represented only by samples of *P.*

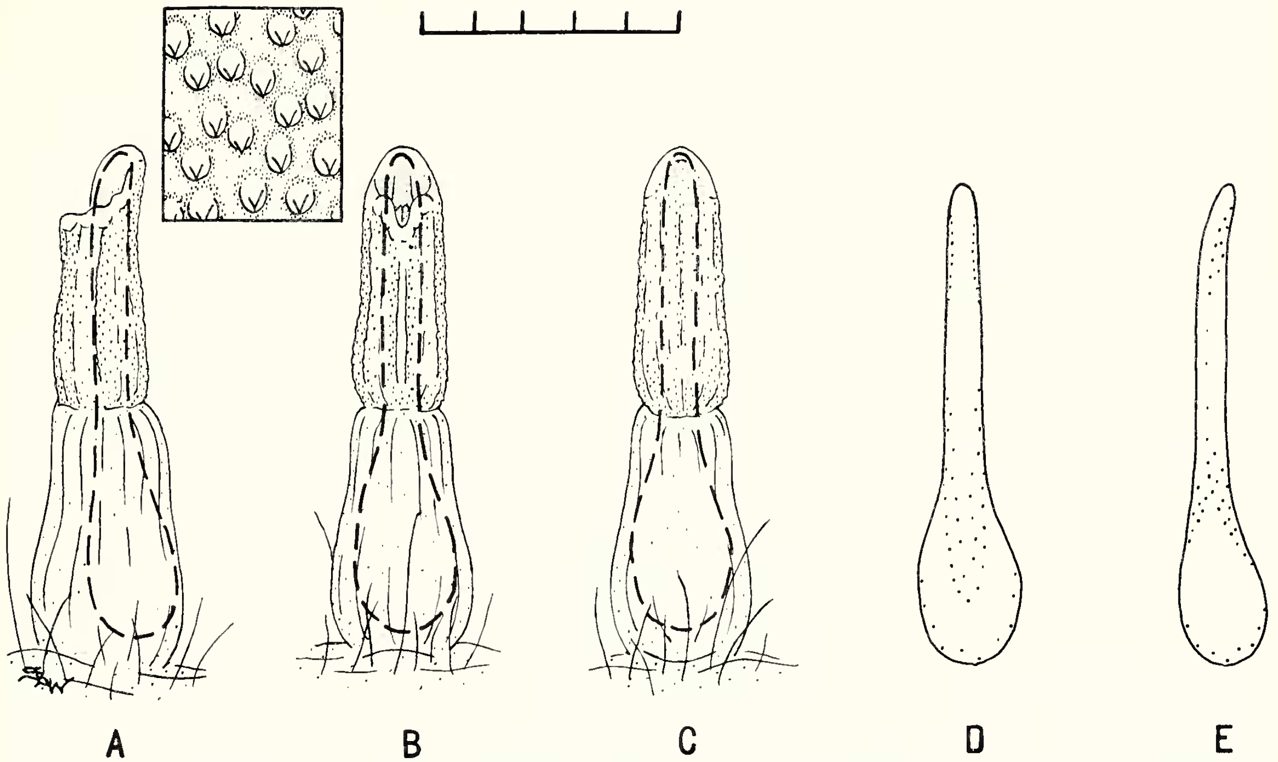

Fig. 22.—Phallus and baculum of *Pappogeomys bulleri bulleri* from Jalisco: 14 mi NW Mascota, 6,400 ft (KU 111714), illustrated as in Fig. 1.

bulleri. All phalli of *P. bulleri* examined were removed from museum specimens and normal restoration was assumed.

The phallus of *P. bulleri* (Fig. 22) has a distal tract about five times longer than its width and about twice as long as the glans. The length of the distal tract ranged from 8.7 to 10.4 mm in adult specimens examined. The sides of the glans, viewed dorsoventrally, are more or less parallel or slightly converging apically. From a lateral view, the dorsal and ventral sides tend to be more recurved. The collar is most apparent on the dorsal side, but loses its distinctness as it extends laterally and apically. Occasionally traces of the collar can be observed on the dorsal side. The pair of urethral processes are barely visible because of their position under the collar. Typical features of geomyid rodents are poorly developed in *P. bulleri*. A midventral raphe is present but not always distinct. The middorsal groove and dorsal protuberances may be present but never well-developed. These features might be more obvious if fresh samples are examined.

Epidermal structures in *P. bulleri* have a single, proximally oriented projection. The size and pattern of structures are fairly uniform. The structures are present on the entire glans, except distal to the collar on the ventral side and along the extreme margins of the apex.

The baculum of *P. bulleri* (Fig. 22) is typical of geomyid rodents. It consists of a bulbous base, slender shaft, and tip. Viewed dorsoventrally, the base gradually tapers to the shaft. The length of the baculum in adult specimens examined ranged from 7.8 to 9.4 mm. The baculum is slightly curved.

The ratio of the condylobasal length to the length of the distal tract and the length of the baculum ranges from 3.4 to 4.4 and 4.0 to 4.9, respectively. The ratio of the length of the distal tract to the length of the baculum ranged from 1.1 to 1.2.

Samples of *P. bulleri* were included with samples of *Cratogeomys* for statistical analysis because of the close relationship of the taxa as suggested by Russell (1968*b*). Table 6 provides measurements of *P. bulleri* examined in this study.

Specimens examined.—Total (5).

P. b. bulleri (3).—Jalisco: 20 mi SE Autlan, 7,700 ft, 1 (KU); 18 mi (by Carranza Rd.) W Ciudad Guzman, 1 (TTU); 14 mi NW Mascota, 6,500 ft 1 (KU).

Table 6.—*Standard statistics for adult specimens of 17 samples representing one species of* Pappogeomys *and six species of* Cratogeomys.

Taxon	N	Mean	Range ± 2 SE	CV
		Length of distal tract		
Pappogeomys bulleri bulleri	2	9.5	(8.7–10.4) ± 1.71	12.7
Pappogeomys bulleri infuscus	1	10.1		
Pappogeomys bulleri lutulentus	1	10.2		
Cratogeomys castanops castanops	1	11.4		
Cratogeomys castanops perplanus	12	11.4	(10.3–12.9) ± 0.43	6.5
Cratogeomys castanops pratensis	1	11.5		
Cratogeomys castanops rubellus	1	11.7		
Cratogeomys fumosus	2	16.3	(15.3–17.3) ± 2.01	8.7
Cratogeomys gymnurus gymnurus	1	20.2		
Cratogeomys gymnurus russelli	3	15.9	(15.3–16.3) ± 0.59	3.2
Cratogeomys gymnurus tellus	1	16.0		
Cratogeomys merriami irolonis	2	15.5	(15.3–15.8) ± 0.50	2.3
Cratogeomys merriami merriami	2	16.1	(15.8–16.3) ± 0.50	2.2
Cratogeomys tylorhinus angustirostris	5	16.9	(15.6–17.8) ± 0.73	4.9
Cratogeomys tylorhinus planiceps	1	12.5		
Cratogeomys tylorhinus tylorhinus	1	15.8		
Cratogeomys zinseri	2	14.1	(13.2–14.9) ± 1.71	8.5
		Length of glans		
Pappogeomys bulleri bulleri	2	4.9	(4.7–5.2) ± 0.50	7.2
Pappogeomys bulleri infuscus	1	5.5		
Pappogeomys bulleri lutulentus	1	5.4		
Cratogeomys castanops castanops	1	6.3		
Cratogeomys castanops perplanus	12	6.3	(5.8–7.1) ± 0.23	6.4
Cratogeomys castanops pratensis	1	6.5		
Cratogeomys castanops rubellus	1	6.4		
Cratogeomys fumosus	2	8.5	(8.4–8.6) ± 0.20	1.7
Cratogeomys gymnurus gymnurus	1	10.9		
Cratogeomys gymnurus russelli	3	8.8	(8.2–9.1) ± 0.57	5.6
Cratogeomys gymnurus tellus	1	9.2		
Cratogeomys merriami irolonis				
Cratogeomys merriami merriami	2	9.3	(8.8–9.9) ± 1.10	8.4
Cratogeomys tylorhinus angustirostris	6	9.4	(8.7–10.1) ± 0.44	5.8
Cratogeomys tylorhinus planiceps	1	6.4		
Cratogeomys tylorhinus tylorhinus	1	8.5		
Cratogeomys zinseri	2	7.3	(6.8–7.7) ± 1.42	8.7
		Length of protractile tip		
Pappogeomys bulleri bulleri	2	1.5	(1.5–1.5) ± 0.00	0.0
Pappogeomys bulleri infuscus	1	1.9		
Pappogeomys bulleri lutulentus	1	1.8		
Cratogeomys castanops castanops	1	2.0		
Cratogeomys castanops perplanus	12	2.0	(1.6–2.3) ± 0.11	10.4
Cratogeomys castanops pratensis	1	1.9		
Cratogeomys castanops rebellus	1	1.9		
Cratogeomys fumosus	2	2.5	(2.4–2.5) ± 0.10	2.8
Cratogeomys gymnurus gymnurus	1	3.0		
Cratogeomys gymnurus russelli	3	2.8	(2.5–3.3) ± 0.50	15.6
Cratogeomys gymnurus tellus	1	2.8		
Cratogeomys merriami irolonis				
Cratogeomys merriami merriami	2	3.4	(3.3–3.5) ± 0.20	4.1
Cratogeomys tylorhinus angustirostris	6	2.8	(2.3–3.1) ± 0.28	12.3
Cratogeomys tylorhinus planiceps	1	2.0		
Cratogeomys tylorhinus tylorhinus	1	2.6		
Cratogeomys zinseri	2	2.0	(2.0–2.0) ± 0.00	0.0

Table 6.—*Continued*

Taxon	N	Mean	Range ± 2 SE	CV
		Width of glans across collar		
Pappogeomys bulleri bulleri	2	1.8	(1.6–2.0) ± 0.40	15.7
Pappogeomys bulleri infuscus	1	2.0		
Pappogeomys bulleri lutulentus	1	1.5		
Cratogeomys castanops castanops	1	2.8		
Cratogeomys castanops perplanus	12	2.5	(2.3–2.7) ± 0.10	7.1
Cratogeomys castanops pratensis	1	2.8		
Cratogeomys castanops rebellus	1	2.5		
Cratogeomys fumosus	2	3.0	(3.0–3.0) ± 0.00	0.0
Cratogeomys gymnurus gymnurus	1	3.7		
Cratogeomys gymnurus russelli	2	2.9	(2.9–3.0) ± 0.10	2.4
Cratogeomys gymnurus tellus	1	3.1		
Cratogeomys merriami irolonis				
Cratogeomys merriami merriami	2	2.3	(2.2–2.4) ± 0.20	6.1
Cratogeomys tylorhinus angustirostris	6	3.6	(3.2–4.0) ± 0.27	9.1
Cratogeomys tylorhinus planiceps				
Cratogeomys tylorhinus tylorhinus	1	2.9		
Cratogeomys zinseri	2	3.5	(3.4–3.6) ± 0.20	4.0
		Width of glans across base		
Pappogeomys bulleri bulleri	2	1.6	(1.5–1.7) ± 0.20	8.8
Pappogeomys bulleri infuscus	1	1.5		
Pappogeomys bulleri lutulentus	1	1.7		
Cratogeomys castanops castanops	1	2.8		
Cratogeomys castanops perplanus	12	2.5	(2.3–2.7) ± 0.10	6.9
Cratogeomys castanops pratensis	1	2.7		
Cratogeomys castanops rubellus	1	2.3		
Cratogeomys fumosus	2	3.1	(3.0–3.3) ± 0.30	6.8
Cratogeomys gymnurus gymnurus	1	3.7		
Cratogeomys gymnurus russelli	2	3.3	(3.2–3.4) ± 0.20	4.3
Cratogeomys gymnurus tellus	1	4.2		
Cratogeomys merriami irolonis				
Cratogeomys merriami merriami	2	2.9	(2.8–2.9) ± 0.10	2.4
Cratogeomys tylorhinus angustirostris	6	3.9	(3.5–4.5) ± 0.28	8.7
Cratogeomys tylorhinus planiceps				
Cratogeomys tylorhinus tylorhinus	1	3.2		
Cratogeomys zinseri	2	3.2	(3.2–3.2) ± 0.00	0.0
		Length of baculum		
Pappogeomys bulleri bulleri	2	8.6	(7.8–9.4) ± 1.60	13.1
Pappogeomys bulleri infuscus	1	8.7		
Pappogeomys bulleri lutulentus	1	8.7		
Cratogeomys castanops castanops	1	9.5		
Cratogeomys castanops perplanus	11	10.2	(9.1–10.8) ± 0.31	5.0
Cratogeomys castanops pratensis	1	10.5		
Cratogeomys castanops rubellus	2	9.9	(9.9–10.0) ± 0.10	0.7
Cratogeomys fumosus	2	13.1	(12.9–13.3) ± 1.40	19.0
Cratogeomys gymnurus gymnurus	1	16.3		
Cratogeomys gymnurus russelli	3	14.2	(13.9–14.3) ± 0.27	1.6
Cratogeomys gymnurus tellus	1	14.2		
Cratogeomys merriami irolonis	2	14.4	(14.1–14.7) ± 0.60	2.9
Cratogeomys merriami merriami	2	14.4	(14.0–14.8) ± 0.80	3.9
Cratogeomys tylorhinus angustirostris	6	13.7	(12.4–15.5) ± 1.02	9.1
Cratogeomys tylorhinus planiceps	1	12.2		
Cratogeomys tylorhinus tylorhinus	1	12.9		
Cratogeomys zinseri	2	12.1	(11.6–12.6) ± 1.00	5.8

Table 6.—*Continued*

Taxon	N	Mean	Range ± 2 SE	CV
		Width of bacular base		
Pappogeomys bulleri bulleri	3	1.7	(1.3–2.2) ± 0.53	26.9
Pappogeomys bulleri infuscus	1	1.6		
Pappogeomys bulleri lutulentus	1	2.0		
Cratogeomys castanops castanops	1	2.4		
Cratogeomys castanops perplanus	12	2.3	(2.0–2.8) ± 0.14	10.7
Cratogeomys castanops pratensis	1	2.3		
Cratogeomys castanops rubellus	2	2.1	(2.1–2.2) ± 0.10	3.4
Cratogeomys fumosus	2	2.5	(2.5–2.5) ± 0.00	0.0
Cratogeomys gymnurus gymnurus	1	3.5		
Cratogeomys gymnurus russelli	3	3.1	(2.7–3.5) ± 0.47	13.0
Cratogeomys gymnurus tellus	1	3.4		
Cratogeomys merriami irolonis	2	3.0	(2.8–3.2) ± 0.40	9.4
Cratogeomys merriami merriami	2	2.9	(2.7–3.0) ± 0.30	7.3
Cratogeomys tylorhinus angustirostris	6	3.3	(3.0–3.7) ± 0.20	7.5
Cratogeomys tylorhinus planiceps	1	2.8		
Cratogeomys tylorhinus tylorhinus	1	2.7		
Cratogeomys zinseri	2	2.7	(2.7–2.8) ± 0.10	2.6
		Height of bacular base		
Pappogeomys bulleri bulleri	3	1.4	(1.1–1.8) ± 0.42	25.7
Pappogeomys bulleri infuscus	1	1.5		
Pappogeomys bulleri lutulentus	1	1.4		
Cratogeomys castanops castanops	1	1.4		
Cratogeomys castanops perplanus	12	1.7	(1.4–1.9) ± 0.08	8.5
Cratogeomys castanops pratensis	1	1.7		
Cratogeomys castanops rubellus	2	1.6	(1.5–1.7) ± 0.20	8.8
Cratogeomys fumosus	2	2.0	(1.8–2.2) ± 0.40	14.1
Cratogeomys gymnurus gymnurus	1	2.8		
Cratogeomys gymnurus russelli	3	2.3	(2.0–2.7) ± 0.41	15.3
Cratogeomys gymnurus tellus	1	2.4		
Cratogeomys merriami irolonis	2	1.9	(1.9–2.0) ± 0.73	3.7
Cratogeomys merriami merriami	2	1.2	(1.0–1.4) ± 1.42	23.6
Cratogeomys tylorhinus angustirostris	6	2.1	(1.9–2.4) ± 0.17	10.2
Cratogeomys tylorhinus planiceps	1	1.9		
Cratogeomys tylorhinus tylorhinus	1	1.9		
Cratogeomys zinseri	2	1.7	(1.5–2.0) ± 1.50	20.8
		Condylobasal length		
Pappogeomys bulleri bulleri	3	39.3	(37.7–41.6) ± 2.36	5.2
Pappogeomys bulleri infuscus	1	39.0		
Pappogeomys bulleri lutulentus	1	35.0		
Cratogeomys castanops castanops	1	56.3		
Cratogeomys castanops perplanus	12	58.7	(55.2–64.1) ± 1.47	1.1
Cratogeomys castanops pratensis	1	52.3		
Cratogeomys castanops rubellus	2	48.5	(46.5–50.4) ± 3.91	5.7
Cratogeomys fumosus	2	59.9	(59.0–60.8) ± 1.80	2.1
Cratogeomys gymnurus gymnurus	1	72.7		
Cratogeomys gymnurus russelli	3	64.2	(62.9–66.2) ± 2.01	2.7
Cratogeomys gymnurus tellus	1	71.9		
Cratogeomys merriami irolonis	2	66.5	(66.2–66.8) ± 0.60	0.6
Cratogeomys merriami merriami	2	67.3	(67.6–67.9) ± 1.21	1.3
Cratogeomys tylorhinus angustirostris	4	62.4	(62.3–67.6) ± 2.05	3.3
Cratogeomys tylorhinus planiceps	1	61.9		
Cratogeomys tylorhinus tylorhinus	1	63.6		
Cratogeomys zinseri	2	63.8	(62.2–65.4) ± 3.31	3.5

Table 6.—*Continued*

Taxon	N	Mean	Range ± 2 SE	CV
		Length of hind foot		
Pappogeomys bulleri bulleri	3	29.5	(29–30.5) ± 1.00	2.9
Pappogeomys bulleri infuscus	1	30		
Pappogeomys bulleri lutulentus	1	27.5		
Cratogeomys castanops castanops	1	36		
Cratogeomys castanops perplanus	11	39.5	(35–45) ± 1.65	6.9
Cratogeomys castanops pratensis	1	38		
Cratogeomys castanops rubellus	2	32	(32–32) ± 0.00	0.0
Cratogeomys fumosus	2	47.0	(46–48) ± 2.01	3.0
Cratogeomys gymnurus gymnurus	1	56		
Cratogeomys gymnurus russelli	3	48.7	(47–51) ± 2.41	4.3
Cratogeomys gymnurus tellus	1	45		
Cratogeomys merriami irolonis	2	46	(45–47) ± 2.01	3.1
Cratogeomys merriami merriami	2	51.5	(51–52) ± 1.00	1.4
Cratogeomys tylorhinus angustirostris	6	44.8	(41–47) ± 1.89	5.2
Cratogeomys tylorhinus planiceps	1	46		
Cratogeomys tylorhinus tylorhinus	1	43		
Cratogeomys zinseri	2	48	(48–48) ± 0.00	0.0

P. b. infuscus (1).—Jalisco: 7 mi SSW Tequila, 9,000 ft, 1 (KU).
P. b. lutulentus (1).—Jalisco: Sierra de Cuale, 7,300 ft, 1 (KU).

Cratogeomys

Description

The size and shape of the phallus of *Cratogeomys* is more variable among species than *Geomys*, but less variable than *Thomomys*. The length of the distal tract in adult specimens examined ranged from 10.3 to 17.8 mm. Like *Geomys*, the size relationship between the length of the distal tract and body size of individuals of *Cratogeomys* is less variable than that of some species of *Thomomys*. The ratio of the condylobasal length to the length of the distal tract ranges from 3.6 to 5.5. Basically the glans in *Cratogeomys* is unique from other geomyid rodents (except *Pappogeomys*) in that the sides of the glans, viewed dorsoventrally, tend to be parallel or converge apically. Viewed laterally the dorsal side tends to be straight and the ventral side may be straight or recurved with a slight flaring at the collar. The collar is also unique from most other geomyid species. On the ventral side, the collar is distinct and often exhibits some degree of folding. However, as the collar passes around the glans the distinctness of the collar is reduced laterally and is often nonexistent dorsally. In all cases the collar is extended more apically on the lateral sides. In all samples of *Cratogeomys* the constriction is a distinct feature and is often extended apically on the ventral side. Most species also possess well-developed urethral processes, midventral raphe, middorsal groove, and a pair of dorsal protuberances.

The epidermal structures of *Cratogeomys* have a single, proximally oriented projection. In all species of *Cratogeomys*, the epidermal structures occur between the collar and constriction and distal to the collar on the dorsal side.

The length of the baculum in adult specimens examined ranged from 9.1 to 15.5 mm. The baculum of *Cratogeomys*, like *Geomys*, shows little variation in relative size compared to body size. The ratio of the condylobasal length and the length of the distal tract to the length of the baculum ranges from 4.4 to 6.3 and 1.0 to 1.4, respectively. Like other geomyid species, the baculum is positioned in the center, or slightly dorsal to the center, of the phallus, and consists of a distinct base, shaft, and tip. In all specimens examined the base was dorsoventrally compressed.

The following are detailed descriptions of six of the seven recognized species of *Cratogeomys*. Table 6 provides measurements that apply to each description.

Cratogeomys castanops.—The phallus of *C. castanops* (Fig. 23) is medium-sized compared to other members of the genus. The length of the distal tract, which ranged from 10.3 to 12.9 mm in adult specimens examined, is about five times greater than the width and about twice as long as the length of the glans. The sides of the glans, viewed dorsoventrally, tend to be parallel or converge to the apex.

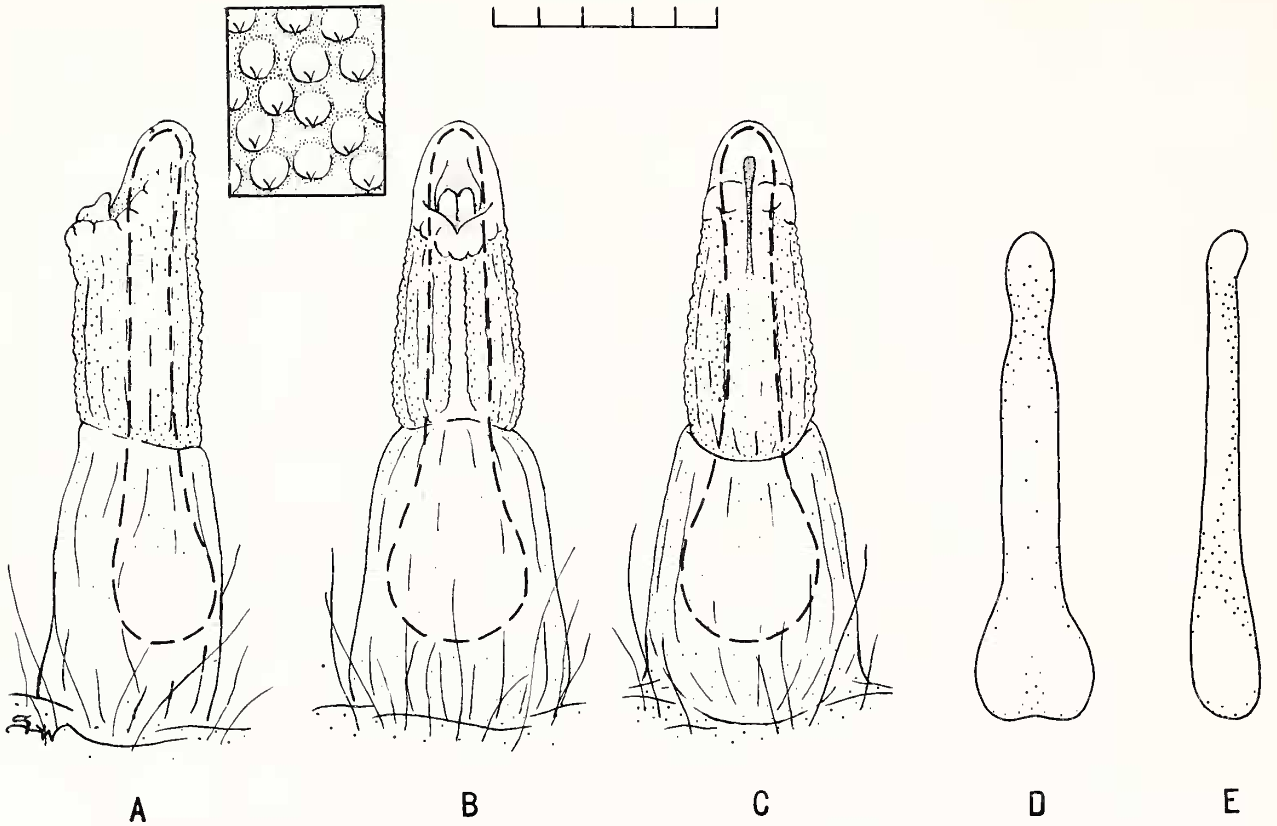

Fig. 23.—Phallus and baculum of *Cratogeomys castanops perplanus* from Texas: Gaines Co., 4.4 mi N, 9.3 mi W Seminole (TTU 25999), illustrated as in Fig. 1.

Viewed laterally the sides are more or less straight and parallel, with a slight flare on the ventral side in the region of the collar. The collar is most distinct on the ventral side and less distinct as it extends apically on the lateral sides. The collar, although poorly developed, may be apparent on the dorsal side. The protractile tip is relatively long. The urethral processes and midventral raphe are well developed. The middorsal groove tends to be short, and the dorsal protuberances are often not distinct.

The epidermal structures of *C. castanops* have a single proximally oriented projection. The size and pattern of structures are uniform.

The length of the baculum ranged from 9.1 to 10.8 mm in adult specimens examined. The baculum of *C. castnops* (Fig. 23), is unique from other geomyid rodents because of its massive appearance. Viewed dorsoventrally there is a distinct base that is straight or slightly concave on the end. The base tapers to a relatively broad shaft that has straight parallel sides. There is a slight indentation of the shaft just proximal to the broad tip. Viewed laterally the base and tip are less evident as they join the shaft to form a relatively straight baculum.

The ratio of the condylobasal length to the length of the distal tract ranged from 4.0 to 5.5; ratio of the condylobasal length to the length of the baculum ranged from 4.7 to 6.3; ratio of the length of the distal tract to the length of the baculum ranged from 1.1 to 1.2.

Specimens examined.—Total (25).

C. c. castanops (1).—COLORADO: *Prowers Co.:* 2.0 mi S, 1.0 mi E Lamar, 1 (TTU).

C. c. perplanus (16).—NEW MEXICO: *Guadalupe Co.:* 1 mi S Santa Rosa, 2 (TTU); *Lea Co.:* 3.3 mi W Crossroads, 1 (TTU); 2.9 mi W Crossroads, 1 (TTU); 2.7 mi W Crossroads, 1 (TTU); 1.4 mi N, 0.5 mi E Maljamar, 1 (TTU); *Roosevelt Co.:* 12.8 mi W Floyd, 1 (TTU). TEXAS: *Bailey Co.:* 5.8 mi S, 0.7 mi W Needmore, 1 (CM); *Deaf Smith Co.:* 1 mi N, 17.9 mi W Hereford, 1 (TTU); 1 mi N, 15.5 mi W Hereford, 1 (TTU); *Gaines Co.:* 4.4 mi N, 9.3 mi W Seminole, 3 (TTU); 4.4 mi N, 6.2 mi W Seminole, 1 (TTU); *Hockley Co.:* 1 mi N, 4.3 mi W Level-

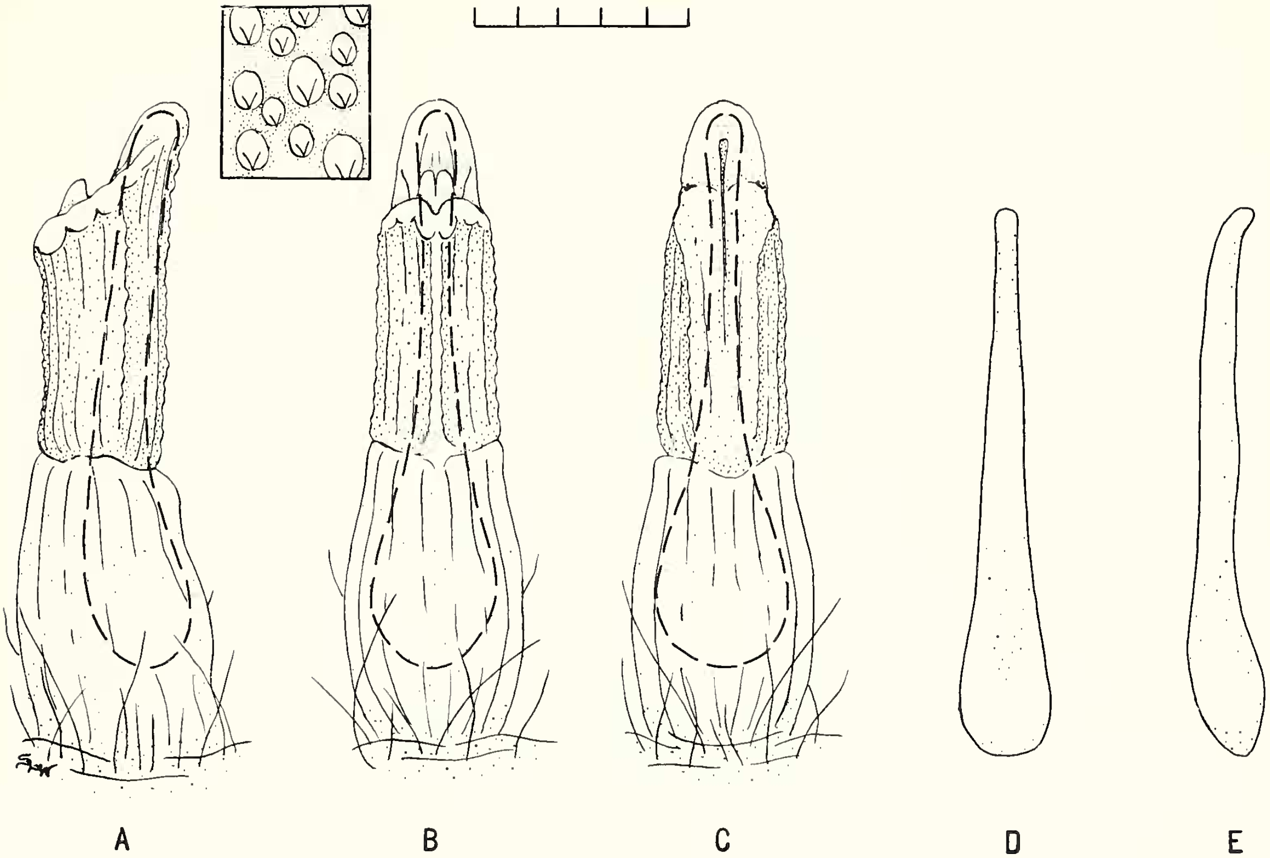

Fig. 24.—Phallus and baculum of *Cratogeomys fumosus* from Colima: 2 mi W Colima (CM 55806), illustrated as in Fig. 1.

land, 1 (TTU); *Randall Co.:* 0.2 mi N, 6.5 mi E Canyon, 1 (TTU).

C. c. pratensis (4).—TEXAS: *Brewster Co.:* 11.8 mi N, 2.0 mi E Marathon, 4,900 ft, 1 (CM); *Jeff Davis Co.:* 9 mi NE Fort Davis, 1 (TTU); *Pecos Co.:* 17.0 mi N, 18.5 mi E Marathon, 4,500 ft, 1 (CM); 14.4 mi N, 18.3 mi E Marathon 4,450 ft, 1 (CM).

C. c. simulans (1).—TEXAS: *Lubbock Co.:* Lubbock airport, 1 (TTU).

C. c. rubellus (3).—SAN LUIS POTOSI: 5.7 mi E Jct. Hwy. 80 and Hwy. 101 near Tepeyac, 1 (TTU). ZACATECAS: 45 km (by road) NE Morelos, 2 (TTU).

Cratogeomys fumosus.—The phallus of *C. fumosus* (Fig. 24), although larger than *C. castanops*, is still considered to be medium-sized. The length of the distal tract is about five or six times greater than the width, and less than twice the length of the glans. The length of the distal tract in two adult specimens examined was 17.3 and 15.3 mm. The shape of the glans and its collar are similar to that of *C. castanops*. Also, as in *C. castanops*, the protractile tip appears relatively long compared to some of the other species of *Cratogeomys*. The midventral raphe and urethral processes are distinct and well-developed. The middorsal groove and dorsal protuberances of *C. fumosus* tend to be more distinct than *C. castanops*.

The epidermal structures of *C. fumosus* have a single, proximally oriented projection. The size of individual structures is variable.

The baculum of *C. fumosus* (Fig. 24), viewed dorsoventrally, has distally converging sides that tend to obscure the position of the tip and base of the baculum. Viewed laterally, the tip and base are more apparent. The baculum is slightly curved and measured 13.3 and 12.9 mm in two adult specimens examined.

For the two adult specimens the ratio of the condylobasal length to the length of the distal tract was 3.7 and 4.0; condylobasal length to the length of the baculum was 4.7 and 4.8; length of the distal tract to the length of the baculum was 1.2 and 1.3.

Specimens examined.—Total (4).

C. fumosus (4).—COLIMA: 2 mi W Colima, 4 (3 CM, 1 TTU).

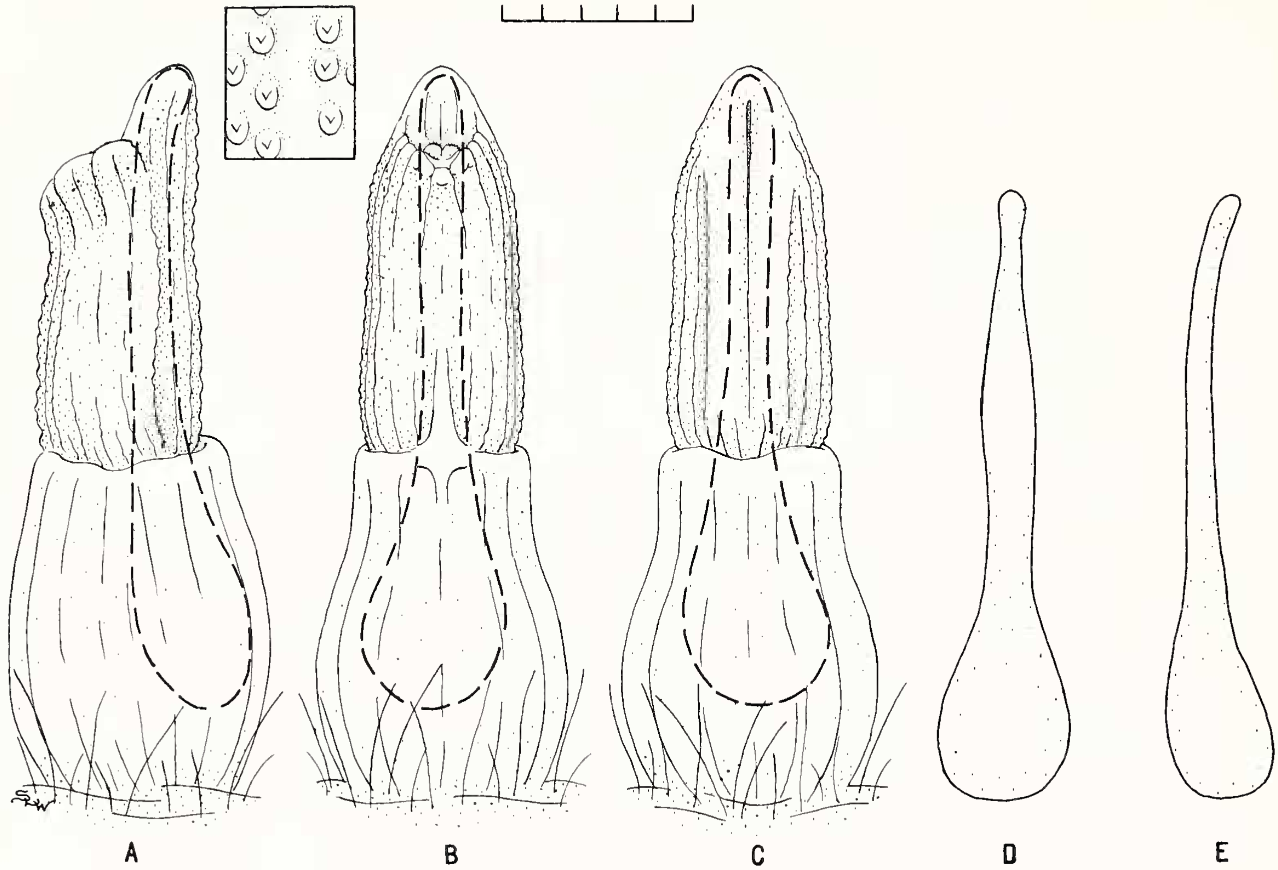

Fig. 25.—Phallus and baculum of *Cratogeomys gymnurus gymnurus* from Jalisco: 3 km S, 14 km W Ciudad Guzman (CM 55812), illustrated as in Fig. 1.

Cratogeomys gymnurus.—The phallus of *C. gymnurus* (Fig. 25) is the largest of the species of *Cratogeomys* examined. The length of the distal tract ranged from 15.3 to 20.2 mm among adult specimens examined. The length of the distal tract is about four to five times greater than its width. The length of the glans is a little more than half the length of the distal tract. The sides of the glans, viewed dorsoventrally, tend to be rather straight and parallel. Viewed laterally the dorsal side is more or less straight and the ventral side is recurved with a flare at the collar. The collar of *C. gymnurus* differs from previously discussed species of *Cratogeomys* in that it appears to be constricted around the urethral opening. Compared to *C. castanops* and *C. fumosus*, *C. gymnurus* tends to have poorly-developed urethral processes. A middorsal groove and dorsal protuberances are present. The shape of the dorsal protuberances are unique from previously discussed *Cratogeomys* in that the pair of protuberances appear to exist for the entire length of the glans. The only indication of a collar on the dorsal side is a slight expansion of the dorsal protuberances in that area.

The epidermal structures of *C. gymnurus* have a small, single, proximally oriented projection. The size tends to be uniform, but not the pattern.

The length of the baculum of *C. gymnurus* (Fig. 25) ranged from 13.9 to 16.3 mm in adult specimens examined. The baculum consists of a large bulbous base, a well-curved shaft that is expanded in the middle, and a distinct tip.

The range of ratios of the condylobasal length to the length of the distal tract and the length of the baculum was 3.6 to 4.5 and 4.4 to 5.1, respectively. The ratio of the length of the distal tract to the length of the baculum ranged from 1.1 to 1.2.

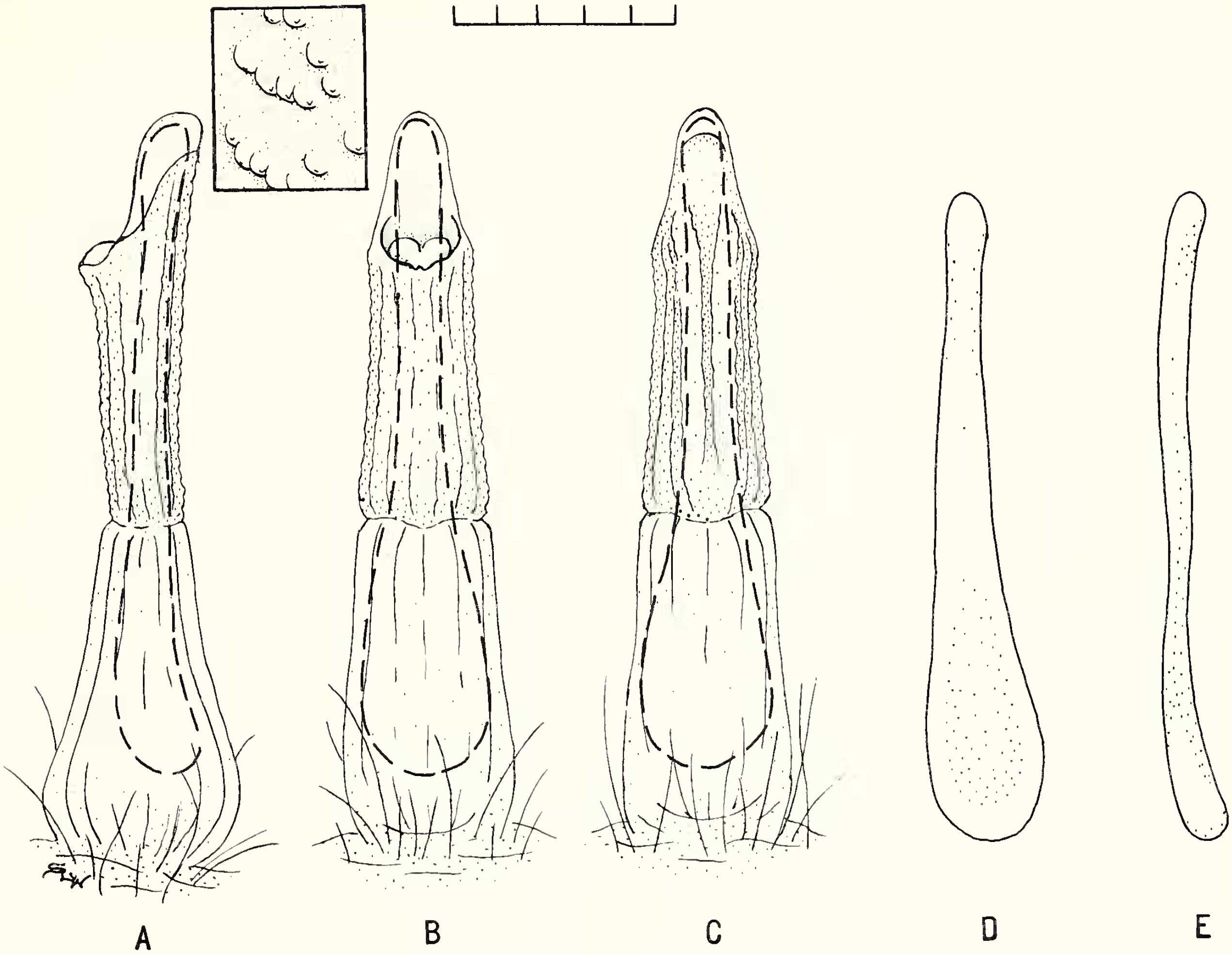

Fig. 26.—Phallus and baculum of *Cratogeomys merriami merriami* from Mexico: 1 km S, 2½ km W Rio Frio, 3,100 m (CM 55815), illustrated as in Fig. 1.

Specimens examined.—Total (10).

C. g. gymnurus (5).—JALISCO: 18 mi W Ciudad Guzman, 2 (TTU); 3 km S, 14 km W Ciudad Guzman, 3 (CM).
C. g. imparilus (1).—MICHOACAN: 8 mi E Opopeo, 1 (TTU).
C. g. russelli (3).—JALISCO: 12 mi S Toleman, 7,700 ft, 3 (KU).
C. g. tellus (1).—JALISCO: 15 mi E Ameca, 1 (TTU).

Cratogeomys merriami.—The phallus of *C. merriami* (Fig. 26) is medium-sized and differs from other species of *Cratogeomys* by its slender appearance. The distal tract is about six times longer than it is wide and less than twice the length of the glans. The length of the distal tract ranged from 15.3 to 16.3 mm in adult specimens examined. The sides of the glans, viewed dorsoventrally, tend to be tapered distally. Viewed laterally, the glans appears narrow in the vicinity of the constriction, where it steadily expands to the region of the collar. The collar is similar to that of other species of *Cratogeomys* but is quite prominent and often lacks convolutions. The long protractile tip is similar to that of *C. castanops* and *C. fumosus*. The urethral processes are unique in that they are mostly attached to the urethral wall, thus restricted to movement. The midventral raphe, if present, is not very distinct. The middorsal groove is usually shallow and broad. A pair of reduced dorsal protuberances is present.

Epidermal structures of *C. merriami* are small and consist of a small single projection. The distribution of the structures tends to follow that of other *Cratogeomys*, but the pattern consists of short, diagonal rows.

The baculum of *C. merriami* (Fig. 26) has a base that tends to be more dorsoventrally compressed than other species of *Cratogeomys*. The specimen illustrated in Fig. 26 demonstrates this feature, but may represent an extreme situation. Viewed dorsoventrally, the baculum is similar to *C. fumosus* in having distally converging sides that obscure the position of the base and tip. The length of the baculum of adult specimens examined ranged from 14.0 to 14.8 mm. These measurements are greater than the baculum length of 13.9 and 13.8 mm reported by Burt (1960). Except for this difference, the descriptions of this study generally agree with those of Burt (1960).

The ratios of the condylobasal length to the length of the distal tract and length of the baculum ranged from 4.2 to 4.3 and 4.5 to 4.8, respectively. The ratio of the length of the distal tract to the length of the baculum ranged from 1.1 to 1.2.

Specimens examined.—Total (12).

C. m. fulvescens (1).—Veracruz: Guadalupe Victoria, 8,300 ft, 1 (TCWC).

C. m. irolonis (3).—Hidalgo: 4 km W Apan, 2 (CM); 2 km N, 3 km W Tepeapulco, 1 (CM).

C. m. merriami (8).—Distrito Federal: 1–8 mi E Sn. Gregoria Altapulco, 2,270 m, 1 (KU); Santa Cruz Acalpixca, 2,270 m, 1 (KU) 4 km W Xochimilco, 2,270 m, 1 (KU). Mexico: 55 km SE Mexico City, 10,500 ft 1 (TCWC); 1 mi SSW Rio Frio, 1 (KU); 1 km S, 2½ km W Rio Frio, 3,100 m, 1 (CM).Tlaxcala: 8 km S, 7 km W Calpulalpan, 2,900 m, 2 (CM).

Cratogeomys tylorhinus.—The phallus of *C. tylorhinus* (Fig. 27) is larger than all other species of *Cratogeomys*, except *C. gymnurus*. The dimensions and features of *C. tylorhinus* are also more similar to *C. gymnurus* than other *Cratogeomys*. The length of the distal tract is four to five times greater than its width. The length of the distal tract ranged from 12.5 to 17.8 mm in adult specimens examined. The length of the glans is more than half the length of the distal tract. Like *C. gymnurus* the sides of the glans, viewed dorsoventrally, are more or less straight and parallel. Viewed laterally the dorsal side is straight for most of its length and the ventral side is recurved with a flaring in the collar region. Also as in *C. gymnurus*, the collar of *C. tylorhinus* is constricted around the urethral opening. The shape and distinctness of most features, including collar, constriction, midventral raphe, middorsal groove, dorsal protuberances, and epidermal structures, are very similar to *C. gymnurus*.

The baculum of *C. tylorhinus* (Fig. 27) is similar to that of *C. gymnurus* by having a large bulbous base, a well-curved shaft that is expanded in the middle, and a distinct tip. The main bacular difference between these species is that *C. tylorhinus* has a slightly smaller baculum with a length ranging from 12.2 to 15.5 mm among adult specimens examined. This range of measurements is greater than the range (10.0–12.5 mm) reported by Burt (1960). However, descriptions of the bacula of this species in this study correspond with those of Burt (1960).

The ratios of the condylobasal length to the length of the distal tract and to the length of the baculum range from 3.7 to 4.9 and 4.5 to 5.1, respectively. The range of ratios of the length of the distal tract to the length of the baculum was 1.0 to 1.4.

Specimens examined.—Total (12).

C. t. angustirostris (9).—Jalisco: 4 mi W Mazamitla, 6,600 ft, 4 (CM); 3 mi WSW Mazamitla, 1 (KU); 5 mi SW Mazamitla, 2 (TTU). Michoacan: Jesus Diaz, W slope Sierra Patamba, 7,500 ft, 1 (KU); 2 mi N Tarequato, 7,200 ft, 1 (KU).

C. t. planiceps (1).—Mexico: El Rio (=San Bernabe), 14 mi NW Toluca, 1 (KU).

C. t. tylorhinus (2).—Hidalgo: ca. 6 mi S Pachuca, 1 (TTU). Mexico: Templo del Sol, Piramida de San Juan Taotihuacán, 1 (KU).

Cratogeomys zinseri.—The phallus of *C. zinseri* (Fig. 28) is considered to be medium-sized compared to the other species of *Cratogeomys*. The length of the distal tract measured 14.9 and 13.2 mm in two adult specimens examined. The length of the distal tract is about four times the width of the distal tract and about twice the length of the glans. The general shape and features of the glans of *C. zinseri* resemble those of *C. gymnurus* and *C. tylorhinus*, with the main difference being a proportionally smaller size. However, the collar region does not appear to be as constricted as in *C. gymnurus* and *C. tylorhinus*. Other features, including the midventral raphe, middorsal groove, and dorsal protuberances, show the same degree of development as those two species. The dorsal protuberances are different in that they lack the expanded region near the collar and apex.

The epidermal structures of *C. zinseri* have a single proximally oriented projection. Although the size of the epidermal structures is uniform, the pattern is not.

The bacula (Fig. 28) of two adult *C. zinseri* measured 12.6 and 11.6 mm. Viewed dorsoventrally the baculum resembles that of *C. gymnurus* and *C. tylorhinus* in having a large base, a shaft expanded in the middle, and a distinct tip. However, the bacu-

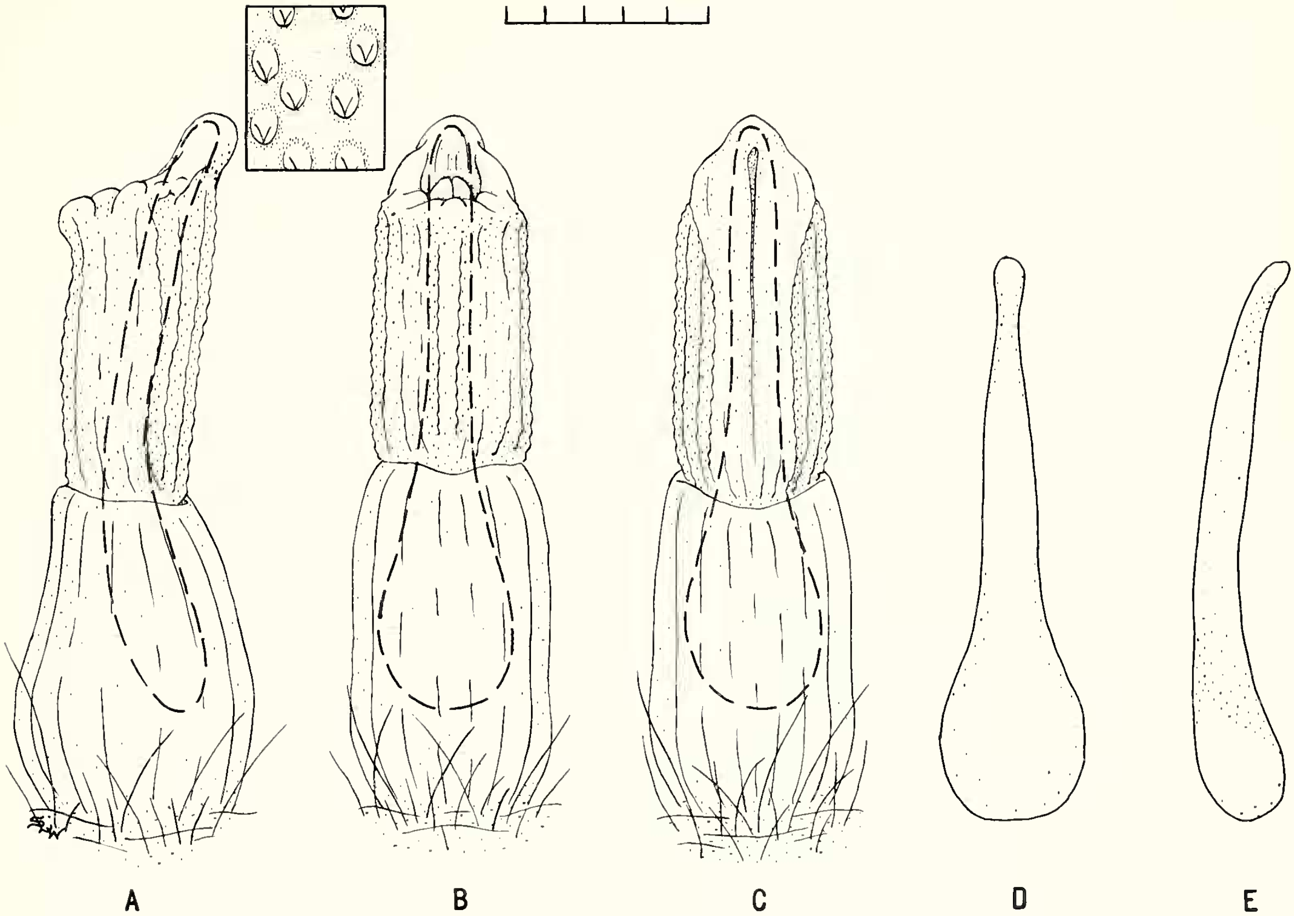

Fig. 27.—Phallus and baculum of *Cratogeomys tylorhinus angustirostris* from Jalisco: 4 mi W Mazamitla, 6,600 ft (CM 55831), illustrated as in Fig. 1.

lum of *C. zinseri* differs from these species by being relatively straighter.

The ratio of the condylobasal length to the length of the distal tract was 4.4 and 4.7; condylobasal length to the length of the baculum was 5.2 and 5.4; length of the distal tract to length of the baculum was 1.1 and 1.2.

Specimens examined.—Total (7).

C. zinseri (7).—JALISCO: Lagos de Moreno, 6,150 ft, 7 (CM).

Statistics

Age variation was observed in phallic characters of *Cratogeomys*. However, analysis and documentation of age variation is beyond the scope of the present study. Table 6 provides standard statistics (sample size, mean, range, standard error, and coefficient of variation) for adult specimens of *Cratogeomys* examined.

Examination of individual variation was conducted on the largest samples of *Cratogeomys* having individuals from the same geographical area that would be assumed to be part of a continuous population. The samples used to examine individual variation were *C. castanops perplanus* from Lea Co., New Mexico, and Gaines Co., Texas (calculated separately from sample of *C. c. perplanus* presented in Table 6 that included a larger geographical area), and *C. tylorhinus angustirostris*. Coefficients of variation of phallic and bacular characters in these two samples ranged from 4.9 to 12.3. The average coefficient of variation for *C. castanops* and *C. tylorhinus* was 7.1 and 8.5, respectively. In both

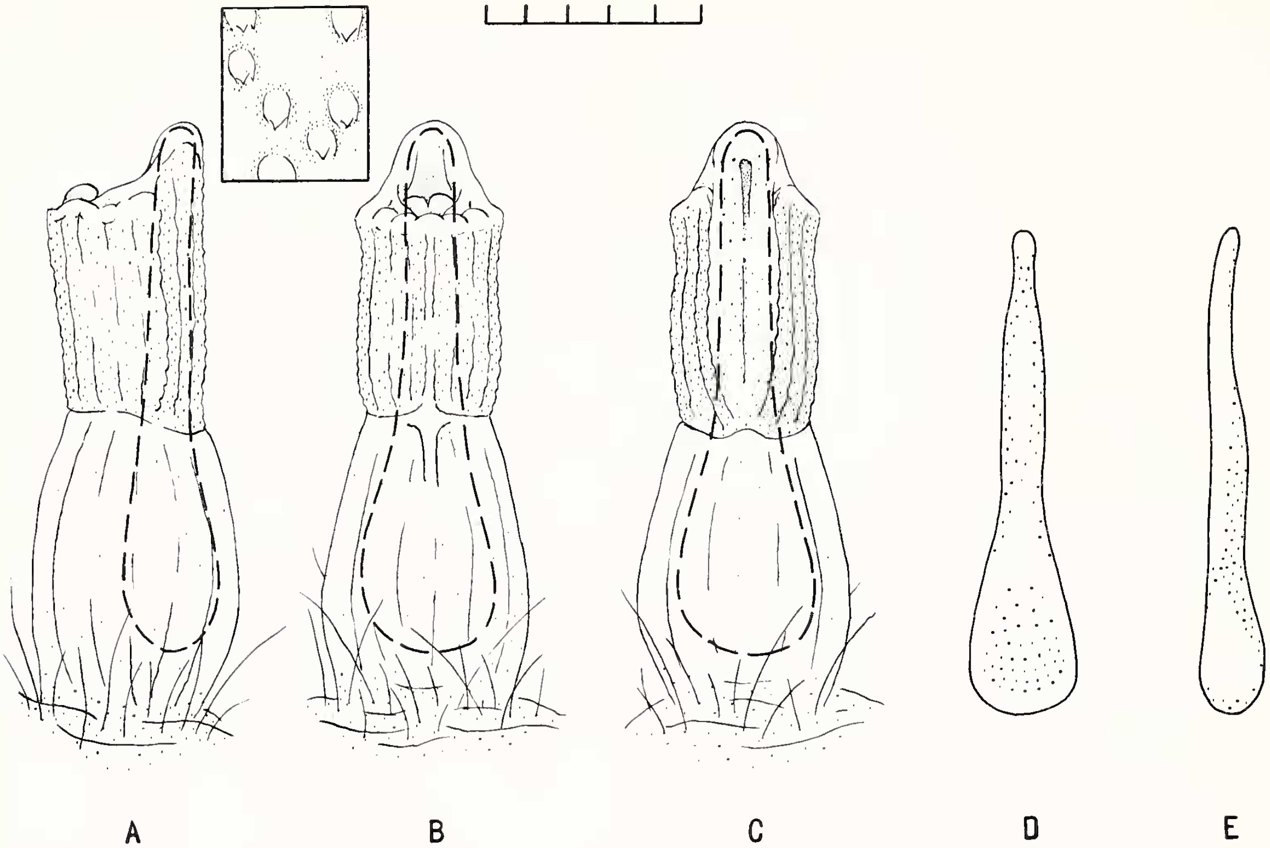

Fig. 28.—Phallus and baculum of *Cratogeomys zinseri* from Jalisco: Lagos de Moreno, 6,150 ft (CM 55848), illustrated as in Fig. 1.

species the length of the distal tract and length of the glans had the lowest values with *C. castanops* having 5.4 and 5.5, and *C. tylorhinus* having 4.9 and 5.8, respectively. The length of the baculum, which had low values in *Thomomys* and *Geomys*, did not rank among the lower values of *Cratogeomys* (6.1 in *C. castanops* and 9.1 in *C. tylorhinus*). In *C. castanops* the width of the glans across base (5.8) was less than the value for the length of the baculum; in *C. tylorhinus* the width of the glans across base (8.7) and width of baculum base (7.5) were less. In both species the length of the protractile tip had the greatest coefficient of variation (8.8 in *C. castanops* and 12.3 in *C. tylorhinus*).

Sample sizes and limited geographical coverage of specimens representing *Pappogeomys* and *Cratogeomys* species examined were inadequate to provide a meaningful analysis of geographic variation within a species. Examination and comparison of measurements of individuals did not reveal the type of variation observed in the genus *Thomomys*.

Examination of variation between *Pappogeomys* and species of *Cratogeomys* was restricted to multivariate analysis, using sample means with the MINT statistical computer program. Samples of a common species were not pooled because the sample sizes were often limited, and combining samples of the same species could lead to a biased representation of the species if geographical variation occurs within the species. The samples of *Pappogeomys* and *Cratogeomys* used in the multivariate analysis, with corresponding number for reference purposes, are three subspecies of *P. bulleri* (*bulleri*, 1; *infuscus*, 2; *lutulentus*, 3), four subspecies of *C. castanops* (*castanops*, 4; *perplanus*, 5; *pratensis*, 6; *rubellus*, 7), *C. fumosus* (8), three subspecies of *C. gymnurus* (*gymnurus*, 9; *russelli*, 10; *tellus*, 11), *C. merriami merriami* (12), two subspecies of *C. tylorhinus* (*angustirostris*, 13; *tylorhinus*, 14), and *C. zinseri* (15).

The distance phenogram produced by the MINT program is illustrated in Fig. 29. The cophenetic

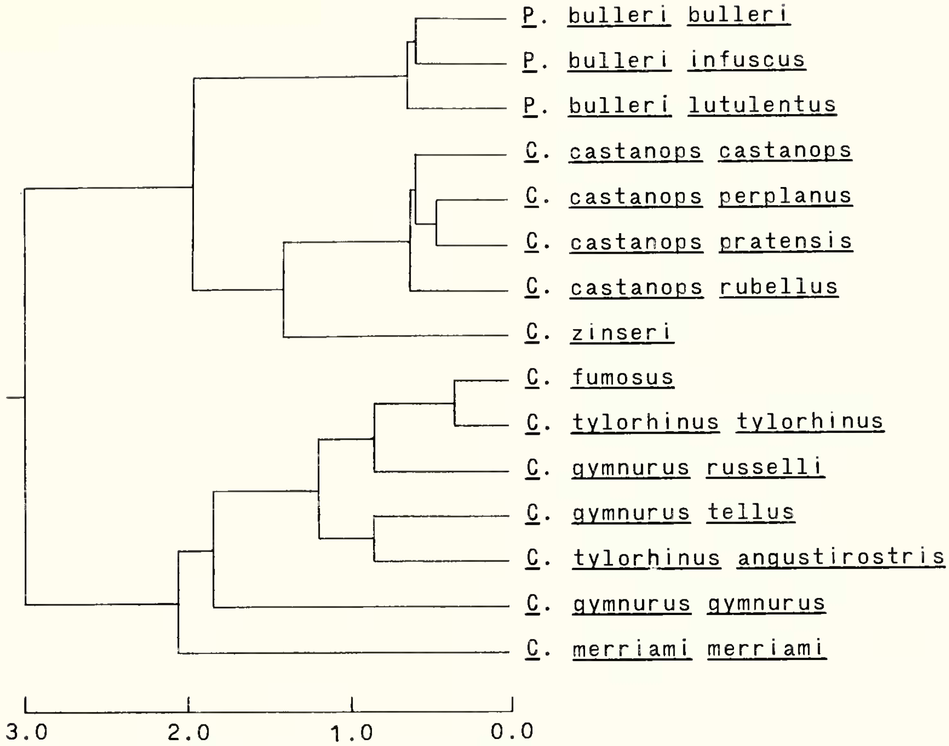

Fig. 29.—Distance phenogram of 15 samples, representing *Pappogeomys* and *Cratogeomys*, resulting from clustering by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.716.

correlation value of the phenogram was 0.716. The phenogram is split into two major groups—one group consisting of *P. bulleri*, *C. castanops*, and *C. zinseri*, and a second group consisting of *C. fumosus*, *C. gymnurus*, *C. merriami*, and *C. tylorhinus*. In the first group all samples of *P. bulleri* cluster together and are separate from all samples of *C. castanops* which also cluster together. *C. zinseri* clusters with the samples of *C. castanops* but is still separate and distinct. In the second group *C. merriami* separates from a cluster including *C. fumosus*, *C. gymnurus*, and *C. tylorhinus*. This final clustering does not conform to taxonomic groups as it did in other parts of the phenogram; *C. fumosus* clusters very closely with *C. t. tylorhinus* and both are grouped with *C. g. russelli*; *C. g. tellus* and *C. t. angustirostris* also form a group together; *C. g. gymnurus* forms a group by itself which is distinct from the rest.

The first three principal components extracted from the matrix of correlation among characters are illustrated in Fig. 30. The three-dimensional projections cluster into three distinct groups along component I. All of the samples of *P. bulleri* (1, 2, 3) form a definite group on the left side. Next all samples of *C. castanops* (4, 5, 6, 7) form a distinct group toward the middle of the plot. The last group consists of broadly scattered projections that represent *C. fumosus* (8), *C. gymnurus* (9, 10, 11), *C. merriami* (12), *C. tylorhinus* (13, 14), and *C. zinseri* (15). *C. zinseri* (15) can be separated from the others with the first component but certainly not by

Table 7.—*Factor matrix from correlation among nine characters of one species (three samples) of* Pappogeomys *and six species (14 samples) of* Cratogeomys *examined.*

Character	Component I	Component II	Component III
Condylobasal length	0.939	−0.015	0.251
Length of distal tract	0.970	−0.101	−0.118
Length of glans	0.979	−0.160	−0.080
Length of protractile tip	0.869	−0.480	−0.026
Width of glans across collar	0.842	0.442	0.223
Width of glans across base	0.945	0.166	0.187
Length of baculum	0.975	−0.163	−0.084
Width of bacular base	0.971	−0.003	0.049
Height of bacular base	0.795	0.401	−0.440

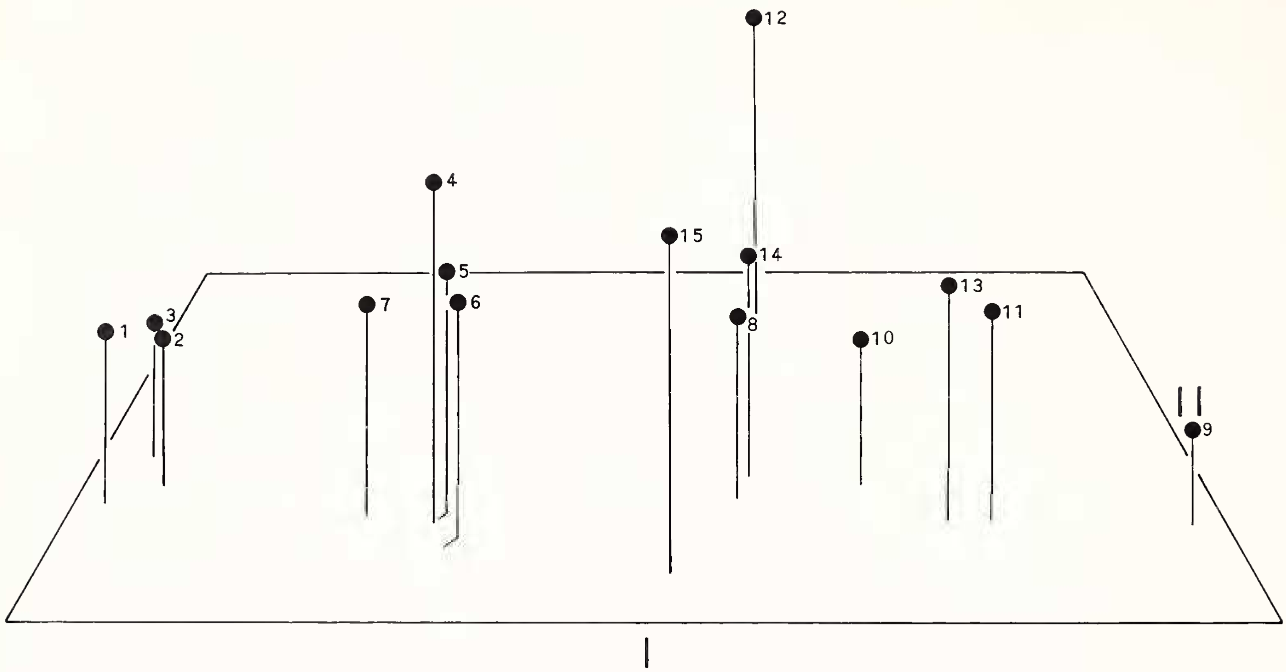

Fig. 30.—Three dimensional projection of 15 samples representing *Pappogeomys* (*P. bulleri*, 1–3) and *Cratogeomys* (*C. castanops*, 4–7; *C. fumosus*, 8; *C. gymnurus*, 9–11; *C. merriami*, 12; *C. tylorhinus*, 13–14; *C. zinseri*, 15) onto the first three principal components based upon a matrix of correlation among one cranial, five phallic, and three bacular measurements. Components I and II are indicated in the plots and component III is represented by height.

the magnitude of *P. bulleri* and *C. castanops*. *C. zinseri* (15) is also separated with component II. *C. merriami* (12) is also separated from the other samples with component II. *C. gymnurus* (9, 10, 11) is distinct from *C. fumosus* along component I but overlaps with *C. tylorhinus* (13, 14) in the first two components and is barely separated with component III. *C. fumosus* (8) and *C. tylorhinus* (13, 14) are separated with component III.

The amount of phenetic variation explained by components I, II, III are 85.2%, 7.5%, and 4.1%, respectively. Results of principal components analyses showing the influence of each character for the first three components are given in Table 7. All characters are heavily weighted in the first factor. In the second factor the characters having the greatest weighing were length of protractile tip of glans, width of glans across collar, and height of bacular base. The height of the bacular base also had the heaviest weighing in the third factor.

DISCUSSION

This study found the phallus and baculum of members of the family Geomyidae to be relatively simple and comparable to *Liomys* (Genoways, 1973), *Reithrodontomys*, and some species of *Peromyscus* (Hooper, 1958, 1959). Throughout the family the basic phallic and bacular features remain uniform. The phallus always includes a glans that is featured with a well-defined collar that marks a conspicuous protractile tip; urethral processes are always present and are situated on the ventral side of the protractile tip; epidermal structures occur on the surface of the glans proximal to the collar and on the dorsal surface of the protractile tip. The baculum always has a simple osseous shaft with some terminal differences indicating the presence of a tip and basal region. These characters typify the family Geomyidae. Additional modification and elaboration of the phallus and baculum, similar to that observed in other rodent families (for example, Sciuridae, Cricetidae, Muridae, or Echymidae), is reduced in geomyid rodents (Burt, 1960; Hooper, 1958, 1959, 1960, 1961, 1962; Hooper and Hart, 1962; Hooper and Musser, 1964; Lidicker, 1968; Williams et al., 1980).

Because the basic phallic and bacular features are relatively uniform in the family Geomyidae, it is difficult to define unique characters that would differentiate the genera. *Thomomys* is the only genus that has representatives (*T. clusius, T. idahoensis, T. mazama, T. monticola,* and *T. talpoides*), with long, narrow phalli and bacula, and phalli and bacula that are large in proportion to body size (as indicated by condylobasal length). However, there are other representatives of the genus *Thomomys* (*T. bottae, T. bulbivorous, T. townsendii,* and *T. umbrinus*) that have similar dimensions and proportions to most members of other genera. At this point, characters (excluding size) such as the width of the collar, distinctness of the collar (particularly from a dorsal view), and number of projections on epidermal structures, are the most useful in further differentiating genera. For instance, *Geomys* and *Zygogeomys* differ from *Thomomys, Orthogeomys, Cratogeomys,* and *Pappogeomys* by having more than a single projection on each epidermal structure. *Pappogeomys, Cratogeomys,* and some species of *Thomomys* typically have a glans that tapers distally. The collar of these species often lacks flaring and is not well-defined dorsally. *Geomys* typically has a collar that is distinct from all aspects and is often the widest part of the glans. Although various characters and combinations of characters can be used for generic identification, it is not possible to select specific features that will typify all members of a genus and differentiate them from all other members of the family. However, in some species, characteristics unique to that species can be used for differentiation from all other members of the family. For instance, the phallus of *Thomomys bulbivorous* and the bacula of *Geomys pinetis* and *Cratogeomys castanops* have features that are distinct and characterstic to the respective taxon.

At the species level, nongeographic and geographic variation contribute to many differences observed in features and dimensions. It is possible that physical problems of working with soft, delicate, anatomical parts could account for some of the variation observed. Because of the variation occurring within a species, identifying phallic and bacular characteristics of any particular species should be based on bacular dimensions and overall morphological features.

In spite of the limitations imposed on selecting discernible characteristics, this study revealed some interesting relationships among species of the same genus. However, it is believed that no systematic conclusions should be based solely on findings in this study. Instead, it is intended that for any taxonomic group, data presented should be used in conjunction with other types of data published by other investigators. In this sense this study presents an approach to systematic problems among pocket gophers that can be useful in providing supportive or refutive arguments for previous systematic studies.

The systematic relationships among the species of *Thomomys* have been speculated by several investigators. Elliot (1903) recognized the uniqueness of *T. bulbivorous* and erected the new subgenus *Megascapheus* to separate it from the other species. Bailey (1915) distinguished species groups of *Thomomys* based on whether the shape of the rostrum was heavy or slender. Although *T. bulbivorous* remained unique it was grouped in the heavy-rostrum species along with *bottae, townsendii,* and *umbrinus*. However, Russell (1968*a*) maintained that *T. bulbivorous* is a group distinct from the heavy-rostrum and slender-rostrum species groups. At the present time arguments presented by Thaeler (1980) probably best represent the relationships among the species at the subgeneric level. Based on chromosome data two species groups are apparent. These data as well as characters used in other studies, such as sphenoid fissure (Durrant, 1946; Hall, 1946; Hall and Kelson, 1959), infraorbital canals (Durrant, 1946), enamel configuration of lower fourth premolar and angular process of ramus (Thaeler, 1980), prompted Thaeler (1980) to propose two subgenera of *Thomomys*—*Thomomys* and *Megascapheus*. The former includes *T. clusius, T. idahoensis, T. mazama, T. monticola,* and *T. talpoides*; the latter includes *T. bottae, T. bulbivorous, T. townsendii,* and *T. umbrinus*.

Data presented in this study concerning the phallus and baculum of *Thomomys* corresponds to the systematic relationships proposed by Thaeler (1980). The subgenus *Thomomys* is characterized by a long, slender and simple phallus, a long baculum with a less distinct base, and a relatively long phallus and baculum compared to body size; the subgenus *Megascapheus* has a shorter, broader, and more complex phallus, a shorter baculum with a distinct base, and a relatively short phallus and baculum compared to body size. Mean ratios of the condylobasal length to the length of the distal tract and length of the baculum, rank the species of *Thomomys* in the following order: *mazama, talpoides, monticola, idahoensis, clusius, bottae, townsendii, umbrinus,* and *bulbivorous.* Clearly the two subgenera do maintain distinct differences in the phallus and baculum. As in previous studies (Elliot, 1903; Russell, 1968*a*) *T. bulbivorous* remains relatively distinct from other species. The phallus is unique in shape, features, and ratio with baculum length. However, the similarities between *T. bulbivorous* and other members of the subgenus *Megascapheus,* as well as data presented by Thaeler (1980), indicate that this species is a member of the subgenus in spite of its uniqueness.

The dimensions of the phallus and baculum of the genus *Thomomys* are extremely variable among species. Although examination of variation within a species was restricted by the few number of subspecies available, this study indicates that considerable variation persists to the subspecific level. It is possible that examination of the phallus and baculum of specimens throughout the range of a species could serve as an indicator of subspecific groups—particularly in *T. talpoides.* In view of the variation in the dimensions of the phallus and baculum of *T. talpoides,* it is interesting that both morphological and metrical data indicate a similarity between *T. monticola* and *T. talpoides.* The similarity is even more intriguing because one of the subspecies of *T. talpoides* that is most similar to *T. monticola* is *T. t. quadratus* which occurs in the same geographical region as *T. monticola* (Thaeler, 1968).

The systematic relationships of species of *Geomys* have been discussed by several investigators with a degree of uncertainty resulting from conflicting data. It is generally accepted that two different groups of *Geomys* exist—the eastern group and the western group. The eastern form, or the *pinetis*-species group previously included *G. colonus, G. cumberlandius, G. fontanelus,* and *G. pinetis* until they were all synonymized under *G. pinetis* by Williams and Genoways (1980). There is some question as to which western species of *Geomys* is most closely related to *G. pinetis.* Russell (1968*a*) suggests that *G. bursarius* and *G. pinetis* differentiated from a common ancestor during the Sangamon time. This assumption is based on examination of the fossil record and cranial characteristics. The fossil record in Florida has led Martin (1974*a*, 1974*b*) and Martin and Webb (1974) to suggest that *G. personatus* and *G. pinetis* are more closely related and could be conspecific. Karyotypic data presented by Davis et al. (1971) and Williams and Genoways (1975) confirms the specific status of each species but does not determine whether *G. bursarius* or *G. personatus* is more closely related to *G. pinetis.* Further questions of systematic relationships of species of *Geomys* occur among the western species—*G. arenarius, G. attwateri, G. bursarius, G. personatus,* and *G. tropicalis.* Morphological and karyological data support the taxonomic status of these species (Davis et al., 1971; Davis, 1940; Hart, 1978; Honeycutt and Schmidly, 1979; Kennerly, 1958, 1959; Merriam, 1895; Tucker and Schmidly, 1981; Williams and Genoways, 1977, 1978, 1981), but different relationships among many of these have been suggested. Cranial characteristics examined by Alvarez (1963) and electrophoretic data presented by Selander et al. (1973) suggest that *G. arenarius* is closely related to *G. personatus* and *G. tropicalis.* Although *G. arenarius* externally and cranially resembles *G. personatus* of the lower Rio Grande Valley, Davis (1940) speculated that *G. arenarius* is more closely related to *G. lutescens* (= *bursarius*) of Texas and New Mexico for physiographic reasons. After examining the fossil record and cranial characteristics, Russell (1968*a*) suggested that *G. arenarius* and *G. personatus* both differentiated independently from *G. bursarius,* probably during the Wisconsin glaciation. Penney and Zimmerman (1976) suggested that both of these species, as well as *G. tropicalis,* differentiated independently and at different times from *G. bursarius.* However, cranial characters (Alvarez, 1963), zoogeography (Selander et al., 1962), and parasite data (Price and Emerson, 1971) indicate *G. tropicalis* has closer affinities to *G. personatus* than *G. bursarius.* Therefore the main systematic questions in *Geomys* concern the relationships of *G. arenarius* and *G. pinetis* to *G. bursarius* or *G. personatus.* Also, the relationship of the recently resurrected *G. attwateri* (Tucker and Schmidly, 1981) to other species of *Geomys* is unknown.

Comments regarding the relationships among species of *Geomys,* based on phallic and bacular characters, are difficult to make because these characters are conservative (particularly when compared to other genera, such as *Thomomys* and *Cratogeomys*). The primary difference observed between species was size, but this feature cannot be considered indicative of any particular species because of geographical variation. Size characteristics might be most useful in comparisons at the level of subspecies. The width of bacular base was particularly useful in differentiating the eastern pocket gophers (*G. pinetis*) and the western pocket gophers (*G. arenarius, G. attwateri, G. bursarius, G. personatus*, and *G. tropicalis*). In this study other similarities among species were best indicated by multivariate analysis, which were able to distinguish some of the species. This analysis supports the recognized subspecific differences of *G. p. streckeri* (Williams and Genoways, 1981), and indicates that both *G. pinetis* and *G. arenarius* are more similar to *G. bursarius* than to *G. personatus*, thus supports work done by Russell (1968*a*). Furthermore, *G. arenarius* is most similar to the closest geographical race of *G. bursarius, G. b. knoxjonesi*. This similarity agrees with comments made by Davis (1940) about the relationships of *G. arenarius*. *G. attwateri* was most similar to *G. bursarius*.

The first comprehensive effort to determine the systematic relationships of the genera *Cratogeomys* and *Pappogeomys* was done by Merriam (1895). The genera (followed by the currently recognized species in parentheses) that Merriam (1895) recognized were *Pappogeomys* (*bulleri*), *Cratogeomys* (*castanops* and *merriami*), and *Platygeomys* (*fumosus, gymnurus*, and *tylorhinus*). It was suggested in that revision that *gymnurus* and *tylorhinus* were very closely related, and that *castanops* could be subgenerically distinct from other *Cratogeomys*. Goldman (1939*a*, 1939*b*) reviewed *Platygeomys* and *Pappogeomys*. In these reviews several new taxa were described, including the currently recognized species *neglectus* and *zinseri* that were named under *Platygeomys*. Hooper (1946) later synonymized *Platygeomys* under the genus *Cratogeomys*. Russell (1968*b*) conducted one of the most comprehensive studies of this group. In that revision *Cratogeomys* (including the *Platygeomys* group) was synonymized under *Pappogeomys*. Under this generic designation the subgenus *Pappogeomys* included *alcorni* (Russell, 1957) and *bulleri* and the subgenus *Cratogeomys* was split into the *castanops* species-group (*castanops* and *merriami*) and the *gymnurus* species-group (*fumosus, gymnurus, neglectus, tylorhinus*, and *zinseri*). In this arrangement Russell (1968*b*) suggested that *gymnurus, tylorhinus*, and *zinseri* are the closest related species of the subgenus *Cratogeomys*. However, electrophoretic data presented by Honeycutt and Williams (1982) create several questions concerning the systematic arrangements suggested by Russell (1968*b*). According to Honeycutt and Williams (1982), the subgenera *Pappogeomys* and *Cratogeomys* (as established by Russell, 1968*b*) deserve generic recognition; *C. castanops* and *C. merriami* are not monophyletic; *C. gymnurus* and *C. tylorhinus* are similar enough to each other to suggest a conspecific relationship. Characteristics and statistical analyses of the phalli and bacula of *Cratogeomys* and *Pappogeomys* found in this study support many of the relationships suggested by other investigators. *Pappogeomys* (represented by *P. bulleri*) is most easily distinguished from *Cratogeomys* by size. Within *Cratogeomys*, each species of the *castanops* species-group (*C. castanops* and *C. merriami*), maintain characteristics (particularly bacular characteristics) and dimensions that differentiate them from other members of the genus. However, the anatomical and metrical differences observed between *C. castanops* and *C. merriami* support Merriam (1895) and Honeycutt and Williams (1982) in that *C. castanops* could be subgenerically distinct from other members of the genus. In the *gymnurus* species-group anatomical characters tend to be more subtle and the main difference among species is size. This is particularly true for *C. gymnurus, C. tylorhinus*, and *C. zinseri*, thus supporting the close similarity of these species (particularly *C. gymnurus* and *C. tylorhinus*) as discussed by Merriam (1895), Russell (1968*b*), and Honeycutt and Williams (1982).

SUMMARY

This study involving the phalli and bacula of the family Geomyidae was intended to serve as an approach to the systematics of the family. Material used in this study included 388 specimens representing all six genera and 24 of the currently recognized species in the family.

The methods used and material available precluded further examination of other problems that

should be investigated. One such problem is the growth and development of the phallus and baculum. It would be very interesting to know about the size and feature changes that occur with maturity to a reproductively active age. Another interesting problem is the detailed documentation of geographic variation of the phallus and baculum of geomyid species that have extensive distributions. It is hoped that data presented in this study will be useful in approaching such problems.

Based on data presented in this study several systematic relationships are suggested, most of which are in agreement with previous investigators. Phallic and bacular data reveal two groups of *Thomomys* which agree with current subgeneric designations. The subgenus *Thomomys* includes *T. clusius*, *T. idahoensis*, *T. mazama*, *T. monticola*, and *T. talpoides*; the subgenus *Megascapheus* includes *T. bottae*, *T. bulbivorous*, *T. townsendii*, and *T. umbrinus*. Although the phallus of *T. bulbivorous* is unique, it is considered to be an extreme case of variation existing in the subgenus *Megascapheus*.

The systematic relationships of *Geomys* indicated by phallic and bacular data reveal two species groups which correspond to geographic distributions. One species-group includes *G. pinetis*; the other species-group includes the western species (*G. arenarius*, *G. attwateri*, *G. bursarius*, *G. personatus*, and *G. tropicalis*). Although data are presented to suggest that *G. pinetis*, *G. arenarius*, and *G. attwateri* have a closer phenetic similarity to *G. bursarius* than any other species of *Geomys*, additional data are needed for a more substantiated systematic arrangement of all species of *Geomys*.

Phallic and bacular differences of the genus *Pappogeomys* (used by Russell, 1968*b*) indicate species groups that are in agreement with taxonomic changes suggested by Honeycutt and Williams (1982). These changes include generic recognition of *Pappogeomys* and *Cratogeomys*. From material examined in this study *Pappogeomys* includes *bulleri*; *Cratogeomys* includes *castanops*, *merriami*, *fumosus*, *gymnurus*, *tylorhinus*, and *zinseri*. Within the genus *Cratogeomys* there are probably three distinct lineages of differentiation that may deserve subgeneric recognition. These lineages include one group consisting of *C. castanops*, a second group consisting of *C. merriami*, and a third group which includes the other species of *Cratogeomys*. In the third group the relationship between *C. gymnurus* and *C. tylorhinus* is considered to be extremely close.

It is reiterated that data presented in this study are not intended to be a sole basis for systematic conclusions. Instead it is hoped that this new information will be useful in determining the systematics of the family Geomyidae when it is used in conjunction with data from other studies.

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